The American Midland Naturalist

Devoted to Natural History

Primarily that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

Editor
Theodor Just, Botany

Associate Editors

Edward Albert Chapin, Washington, D. C. ..... Entomology
Carroll Lane Fenton, Washington, D. C. ..... Paleontology
John Hobart Hoskins, Cincinnati, Ohio ..... Botany
Remington Kellogg, Washington, D. C. ..... Paleontology and Zoology
Marcus Ward Lyon, Jr., South Bend, Ind. ..... Zoology
George Willard Martin, Iowa City, Iowa ..... Mycology
Francis Joseph Wenninger, C.S.C. ..... Zoology

Vol. 21, 1939
(January-May)

UNIVERSITY OF NOTRE DAME
Notre Dame, Indiana

Museums
of
Wilson Ornithological Club

CONTENTS

No. 1, JANUARY, 1939

Plant and Animal Communities—*Edited by Theodor Just*

Plant Associations on Land—*Henry S. Conard* 1
Littoral Marine Communities—*G. E. MacGinitie* 28
Fresh-Water Communities—*Frank E. Eggleton* 56
The Biome—*J. Richard Carpenter* 75
The Individualistic Concept of the Plant Association—*H. A. Gleason* 92
The Unistratal Concept of Plant Communities (The Unions)—*Theodor Lippmaa*....111
The Climax and its Complexities—*Stanley A. Cain* 146
Social Coordination and the Superorganism—*Alfred E. Emerson* 182
On the Analysis of Social Organization among Vertebrates, with Special Reference to Birds—*N. Tinbergen* 210
Analytical Population Studies in Relation to General Ecology—*Thomas Park*.....235
Notes and Discussion:
Records of Terrestrial Isopoda or Sow Bugs from North America—*Melville H. Hatch* 256
Bibliofilm Service in Geological Survey..... 258
Book Reviews 259

No. 2, MARCH, 1939

Taxonomic and Ecological Studies of Eastern Tennessee Bryophytes—*Aaron J. Sharp* 267
Bryophyta of Arctic America. II. Species Collected by J. Dewey Soper, Principally in Southern Baffin Island—*William C. Steere* 355
Actinocheita—*Fred A. Barkley* and *Merton J. Reed* 368
A Phytosociological Study of a Cypress-gum Swamp in Southeastern Louisiana—*Thomas F. Hall* and *William T. Penfound* 378
Effect of Frequent Clipping on Plant Production in Prairie and Pasture—*J. E. Weaver* and *V. H. Hougen*..... 396
Fire in Land Use and Management—*Herbert C. Hanson*..... 415
Preliminary Account of the New Albany Shale Flora—*Charles B. Read* and *Guy Campbell* 435
Notes on the Fossil Flora of Yellowstone National Park with Particular Reference to the Gallatin Region—*H. N. Andrews*..... 454
A Summary of the Fossil Crustacea of the Crustacea of the Order of Stomatopoda, and a Description of a New Species from Angola—*Charles T. Berry*....461
Dispharynx pipilonis, a New Spiruroid Nematode from the Red-Eyed Towhee—*O. Wilford Olsen*..... 472
The Life Cycle of the Frog Bladder Fluke, Gorgoderina attenuata Stafford, 1902 (Trematoda: Gorgoderidae)—*John S. Rankin, Jr.* 476
The Natural History of the Blind Goby, Typhlogobius californiensis Steindachner —G. *E. MacGinitie* 489
Four New Rabbits from the Upper Pliocene of Kansas—*Claude W. Hibbard*..... 506
Central Wisconsin Muskrat Study—*F. N. Hamerstrom, Jr.* and *James Blake*..... 514
Elisha Newton Plank—*John T. Buchholz* 521

Notes and Discussion:
Additions and Amendments to the International Rules of Botanical Nomenclature —*Louis Cutter Wheeler* 526
Book Reviews 530

No. 3, May, 1939

A Survey of the Herpetology of Great Smoky Mountains National Park—*Willis King* 531
An Annotated Bibliography of the Zoology of Tennessee and the Tennessee Valley Region—*Charles S. Shoup* 583
Spirocerca longispiculata n. sp.—*William C. Hill* 636
Hymenolepis scalopi n. sp.—*Richard L. Schultz* 641
North American Rhabdocoela and Alloeocoela—IV. Mesotoma macropenis, New Species, from Douglas Lake, Michigan—*Libbie H. Hyman* 646
Cercariae Infecting Pomatiopsis lapidaria Say—*Donald J. Ameel* 651
Entonyssus ewingi n. sp., an Ophidian Lung Mite—*W. Eugene Hubbard* 657
An Annotated List of the Species of Jassinae Known to Occur in Indiana (Homoptera, Cicadellidae)—*Harry E. Brown* 663
The Breeding Habits of the Silvery Minnow, Hybognathus regius Girard—*Edward C. Raney* 674
Some Effects of Fresh Water on the Fauna of a Marine Harbor—*G. E. MacGinitie* 681
Relations of the Vegetation and Climatic Types in Nuevo Leon, Mexico—*Cornelius H. Muller* 687
Geographical Affinities of the Flora of Ohio—*Isabel Thompson* 730
Postglacial Vegetation of the Driftless Area of Wisconsin—*Henry P. Hansen* 752
A New Species of Agave from Trans-pecos Texas—*Cornelius H. Muller* 763
Notes and Discussion:
Extension of the Known Geographic Range of the Striated Chipmunk (Tamias striatus)—*E. Raymond Hall* 766
Book Reviews 767

Nekrolagus, New Name for Pediolagus Hibbard, not Marelli.

Dr. Remington Kellogg has called to my attention the fact that the name *Pediolagus*, recently proposed by me for a genus of Upper Pliocene rabbits (Amer. Midland Nat., Vol. 21, no. 2, p. 512, March, 1939) is preoccupied by *Pediolagus* Marelli, 1927, (Mem. Jardin. Zool. La Plata, Vol. 3, p. 5, August 12, 1927) in Caviidae. I therefore propose to substitute for *Pediolagus* Hibbard, not Marelli, the new generic name **Nekrolagus,** the genotype becoming *Nekrolagus progressus* (Hibbard).

Dates of Publication

Volume 21, 1939

Number 1 January ..... February 20
Number 2 March ..... May 19
Number 3 May ..... June 7

The American Midland Naturalist

Devoted to Natural History, Primarily
that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

▼

Contents

PLANT AND ANIMAL COMMUNITIES

Edited by Theodor Just

Plant Associations on Land — *Henry S. Conard* 1
Littoral Marine Communities — *G. E. MacGinitie* 28
Fresh-Water Communities — *Frank E. Eggleton* 56
The Biome — *J. Richard Carpenter* 75
The Individualistic Concept of the Plant Association — *H. A. Gleason* 92
The Unistratal Concept of Plant Communities (The Unions) — *Theodor Lippmaa* 111
The Climax and its Complexities — *Stanley A. Cain* 146
Social Coordination and the Superorganism — *Alfred E. Emerson* 182
On the Analysis of Social Organization among Vertebrates, with Special Reference to Birds — *N. Tinbergen* 210
Analytical Population Studies in Relation to General Ecology — *Thomas Park* 235

Notes and Discussion:
Records of Terrestrial Isopoda or Sow Bugs from North America — *Melville H. Hatch* 256
Notes on Two Species of Gastrotricha from Washington — *Melville H. Hatch* 257
Bibliofilm Service in Geological Survey 258
Book Reviews 259

Vol. 21 JANUARY, 1939 No. 1

EDITORIAL STAFF

THEODOR JUST,.....*Botany (Ecology, Taxonomy)*
Editor, University of Notre Dame

EDWARD A. CHAPIN.....*Entomology*
U. S. National Museum, Washington, D. C.

CARROLL LANE FENTON,.....*Invertebrate Paleontology*
Washington, D. C.

JOHN HOBART HOSKINS,.....*Botany (Morphology, Paleobotany)*
University of Cincinnati, Cincinnati, Ohio

REMINGTON KELLOGG,.....*Vertebrate Paleontology and Zoology*
U. S. National Museum, Washington, D. C.

MARCUS WARD LYON, JR.,.....*Mammalogy*
South Bend, Indiana

GEORGE WILLARD MARTIN,.....*Mycology*
State University of Iowa, Iowa City, Iowa

FRANCIS JOSEPH WENNINGER, C.S.C.,.....*Invertebrate Zoology*
University of Notre Dame

NOTE:—THE AMERICAN MIDLAND NATURALIST, published from the biological laboratories of the University of Notre Dame, is primarily, though not exclusively devoted to the Natural History of the Middle West. A wide selection of papers on botany, paleontology and zoology is published in bi-monthly issues, six of which make up a volume.

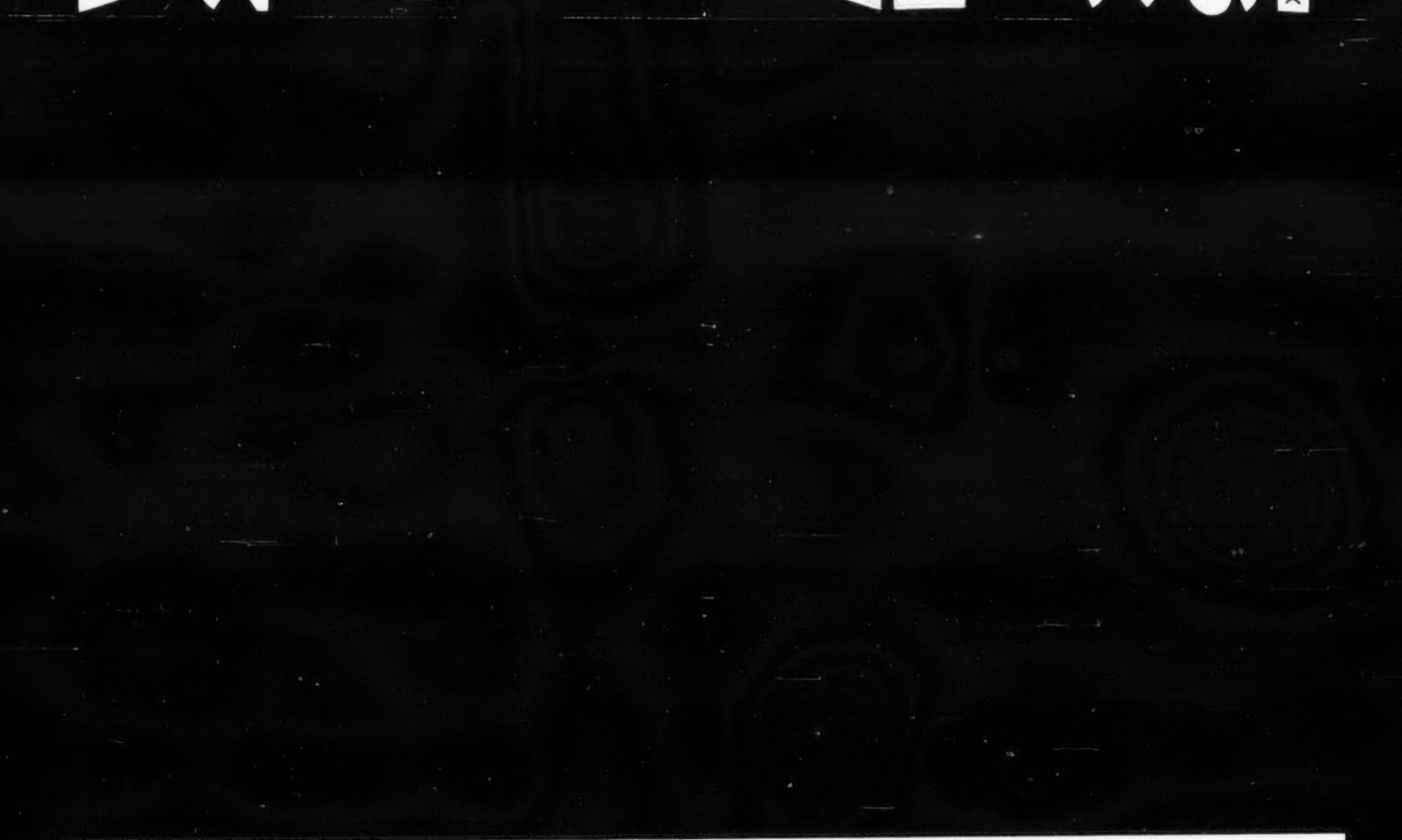
Fifty reprints will be furnished free of charge to contributors. Additional reprints should be ordered when proof is returned and may be had at cost price. Authors are requested to submit abstracts with their manuscripts.

The following numbers are out of print: vol. 2, (1-3, 8-10); vol. 3, (1-3, 5-12) index, title page; vol. 4, (1-7) index, title page; vol. 6, (5, 8) index, title page; vol. 9, (9); vol. 10, index, title page; vol. 11, (1). All others available, 30 cents per copy. Complete volumes: $3.00; volumes 7, 13, and 14, $1.50 each; vol. 15 $2.00, single issues 35 cents; vol. 16 $3.00, single issues 50 cents; vol. 17 $4.50, part 1 $2.00, nos. 2-6 50 cents each; vol. 18 $3.00, single issues 50 cents; vol. 19 $2.50, vol. 20 $2.50, single issues $1.00.

Exchanges for journals, special volumes or duplicate books, and specimens, should be arranged directly through the editorial office at the University of Notre Dame, where subscriptions also are received. Offers should accompany request for exchange.

For citation use this abbreviation: *Amer. Midl. Nat.*

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103, Act of October 3, 1917, authorized on July 3, 1918.



Plant and Animal Communities

Comprising the Proceedings of the Conference on Plant and Animal Communities, held at the Biological Laboratory, Cold Spring Harbor, Long Island, New York, from August 29 to September 2, 1938

Edited by Theodor Just

EDITOR'S PREFACE

Despite an overwhelming amount of available data and observations considerable disagreement still exists in ecological quarters regarding the status and delimitation of the fundamental entity of community study. It is this lack of an all-inclusive concept acceptable to ecologists of the most divergent tastes and interests that prompted the Secretary to call this Conference with the hope of paving in some way the road towards an ultimate understanding.

No aim at exhaustive treatment is claimed but rather a deliberate effort to present a cross section of current concepts with suggestions for future work. In this sense, the book tries to bridge the wide gaps existing particularly between cis- and transatlantic ecology, between the botanical and zoological aspects, and to establish once more the common needs and problems. Moreover, no optimistic notions are entertained about the imminent solution of the continually increasing difficulties. Yet definite achievements are recorded. Thus the book is in no way the equivalent of a text in this biological domain though it is hoped that its comprehensive character and retrospective as well as prospective attitude may recommend it for use in conjunction with such.

The discussions appended to each contribution represent excerpts of all that was said, a treatment necessitated by obvious limitations of space and the unavoidable circuitous nature of some. However, the editor attempted to retain the pertinent comments and to correlate them properly. It was found feasible to use merely the surname of each speaker participating in the discussions.

It is very gratifying to acknowledge here the cooperation received upon invitation from Dr. G. F. Gause, Professor of Experimental Zoology, Moscow, U.S.S.R., for his succinct discussion of analytical population studies and their value in general ecology.

The Conference was conceived and ably directed by its Secretary, Dr. Stanley A. Cain, and made possible through the courtesy of Dr. Eric Ponder, Director of the Biological Laboratory, Cold Spring Harbor, Long Island, N. Y.

THEODOR JUST.

January 31, 1939

The American Midland Naturalist

Published Bi-Monthly by The University of Notre Dame, Notre Dame, Indiana

VOL. 21 JANUARY, 1939 No. 1

Plant Associations on Land

Henry S. Conard

Introductory

The earth is populated by an innumerable host of plants and animals, no two of which, it is generally agreed, are exactly alike. Happily they do have such likenesses as enable us to classify them into less and more inclusive categories. The objects are discovered by us. Their likenesses are discovered. The degrees of likeness and difference are discovered. And on these discoveries our categories are based.

The names of the categories we invent. The evaluation of the likenesses and differences is highly subjective, as indeed the word value implies. If there is any test of such values, it must be the discovery of the usefulness of the categories for purposes of thought — for the using and the increase of knowledge.

By this test of usefulness for purposes of thought every system of classification has its values. It is valuable to its users. Some other scheme might be even more valuable. Thus schemes are tried and gain more or less wide acceptance. Perhaps for a long time one system prevails to the exclusion of all others, as was true of the binomial system of nomenclature.

At least in the testing stage one's sense of values depends upon experience and training. With those who break new paths in the realm of description and classification experience is the thing that counts. Thus a knowledge of the field in which a genius has worked, along with his historic background, gives an understanding or explanation of the viewpoints of the genius.

Of the many workers who have studied natural vegetation we may single out a few who seem to have had especial influence upon contemporary thought, description and classification. It might be well to speak rather of schools than of persons. Thus we should consider the Zürich-Montpellier School, the Scandinavian School, the Danish School, the Russian School, the Chicago School, and the Nebraska School.

The Zürich-Montpellier School

For the Zürich-Montpellier School one must go back to Kerner and his "Pflanzenleben der Donauländer." This beautiful description is a literary as well as a scientific classic. Kerner sketched with permanent precision the major lineaments of central European vegetation. The pronounced differences in vegetation from place to place in old Austria were conspicuous without an

airplane. Kerner presents the Hungarian Puszta — a grassland surprisingly like our own prairies, and still unsettled and unbroken in 1860; the prairie marshlands; the broadleaf forest of the foothills; the needleleaf forests of the mountains; the subalpine Mugho pines; the alpine meadows.

The visibly different plant communities he called Formations. Some of them he designated by a genus name with the suffix *-etum*. It is not surprising therefore that when five years ago an American botanist burst forth in alarm over the "new" terminology, a European botanist referred (in litt.) to the term *-etum* as "a part of the vernacular."

Kerner's use of the term Formation may be shown by citing examples. In the sandy plains of the Baltic region is the Calluna vulgaris formation. In the Pannonian lowlands are four tall-grass formations: Pollinia Gryllus formation, Stipa formation *(S. capillata, S. pennata)*, Bromus formation, and a desert formation. Quotations will indicate the amount of detail he introduces, and a picture of the plant community itself.

Four plant formations especially command our attention in the sands of the Pannonian lowlands. In the first of these the Goldbeard (Pollinia Gryllus) gives the name and the character to the formation. This is a most beautiful grass. It forms almost impenetrable sods, which stand several inches above the dark humus-laden sand, like marmot mounds, beset with harsh grey dead leaves. At the height of your head the violet tinted branches of the panicle spread out, from which hang hair-like, curved and crinkly threads bearing the flowers at their tips. A long bent awn extends from the tip of each spikelet. The violet and steel-blue scales of the spikelet shine with a metallic luster, and at the base of the spikelet a circlet of delicate shiny yellow hairs glitters like gold. These panicles and spikelets crowd one another in thousands at an even height above the ground. They shake and shimmer and bow and nod upon their tall and slender straws. And along with each stem and each panicle the whole grass-covered plain billows and glows in the breath of the wind and the light of the sun. Beneath these panicles and between the sods of this grass some 75 species of other plants crowd in. Of these at least 32 are butterfly flowers, 10 orchids, 11 bulbous plants, and a wealth of other pretty and colorful species. These are definitely arranged in an under layer of low herbs and an upper layer of luxuriant tall herbs. (The appendix lists 51 of these species, without comment.)

Farther on we read:

The three plant formations described above are not always sharply set apart from one another. Oftimes they merge together and give thus a series of characteristic intermediate stages. This merging is of the greatest interest, for it shows on careful observation that the three plant formations have a definite genetic relationship, and that they are really only the developmental stages of a Vegetation which is gradually spreading its verdant flowery carpet over the white sands of the Puszta.

Kerner described in three pages the structure and development (after clearing) of the Beechwood Formation, with three lists of herbaceous plants found in three stages of the succession. The pinewood receives five pages. The appendix gives the following distribution of the more important components of this Formation:

1. Unterste Schichte: Gefilz: *Dicranum scoparium, Hypnum Schreberi, H. cupressiforme, Hylocomium splendens, H. triquetrum, Cladonia rangiferina, C. furcata, C. squamosa.*
   Geblätt und Gekräut: *Cyclamen europaeum, Hepatica triloba, Veronica officinalis, Galium silvestre, Thymus serpyllum, Gnaphalium dioicum.*
2. Schichte: Niederes Gesträuch: *Calluna vulgaris, Vaccinium vitis-idaea, V. myrtillus, Genista pilosa, G. germanica, G. tinctoria, Cytisus capitatus, C. nigricans.*

Gekräut: *Trifolium alpestre, Inula hirta, Melampyrum pratesne, Jasione montana, Dianthus deltoides, Carlina vulgaris, Pyrola secunda, P. umbellata.*

3. Schichte: Gehälm: *Luzula albida, Aira flexuosa, Anthoxanthum odoratum, Brachypodium pinnatum.*
4. Schichte: Hohes Gesträuch: *Juniperus communis, Rubus* spp.
   Gefarn: *Pteris aquilina.*
5. Obere Schichte: Gehölz: *Pinus silvestris.*

With similar charm of expression Schröter has described "Das Pflanzenleben der Alpen." This is clearly a development in great detail of Kerner's chapter on the same subject. The tendency is toward autecology rather than synecology. Rübel, Braun-Blanquet, Lüdi and others have greatly refined ecological research and description in their development of Plant Sociology. The excellence of their work and the extensive fitness and suggestiveness of their method has won such wide approval that their definition of the Association was almost unanimously adopted by the VI International Botanical Congress.

The background of the Zürich-Montpellier School is the magnificent plant mosaic of central Europe and the Alps. The conspicuous feature is the stability of vegetation when left to itself. Braun-Blanquet is impressed with the prevalence of "terminal stages of great stability." By no means denying the reality of vegetational change, the Association is actually found to be extremely permanent in terms of human history. And European history is long! Human intervention is the chief cause of disturbance in the vegetation. And where the hand of man holds firmly, vegetation persists through centuries in anthropogenic stability. A Dutch botanist asked me if the American prairies are not really man-made!

Thus the Association, defined by its floristic composition, is the unit actually found in nature, and upon which all phytosociologic study centers.

In English law a tract of real estate includes all of space above the surface of the plot, and all below, to the center of the earth. Similarly the Association is described not only by the plants, but also by the topographic, climatic, edaphic and biotic conditions. Soil development is particularly important. For the soil profile is the product of the action of vegetation upon the substratum through hundreds or thousands of years. It changes but slowly, whereas various agencies may produce radical and cataclysmic changes in vegetation. The soil profile often gives a permanent record which is highly trustworthy.

The Scandinavian School

In contrast with the luxuriant vegetation of central Europe, the vegetation of marginal lands is conspicuously different. Lands may be marginal because of heat or cold, dryness or wetness, or perhaps because of salinity or barrenness or instability of the substratum.

In northwestern Europe, Ireland to Scandinavia, cold and moisture combine to make marginal conditions. Trees exist miserably or are absent entirely. The most luxuriant growth is of mosses and lichens, followed by grasses,

sedges and heathers. Nordhagen's photograph of a "birch forest" in the Sylene National Park (Fig. 64, 66) is actually pathetic! Even the rich forests of Finland and northwest Germany are in constant danger of reversion to Sphagnum bog, owing to the luxuriance of that moss. Vast quantities of peat accumulate in these cold wet climates. On the level top of a five-foot-cube boulder near Killarney I found four inches of structureless black peat, penetrated by the roots of *Erica carnea* and other plants which densely covered it. The mountains of Ireland are treeless. They are covered with heather and peat. In Scotland one finds a peat bed, not a boulderfield, at the top of the mountain (Grout in litt.). Light and shade are of less consequence in the north than in middle latitudes, partly because there is so little of either. Moss layers and low shrub layers may flourish in a wide variety of circumstances. The soil is almost wholly composed of acid residues of plant decay. Hence come two oft repeated emphases:

1. Soil is a product of vegetation, and is independent of the nature of the substratum.

2. The fundamental unit of vegetation is the layer or synusia (union, sociation).

In a climate which is only really fit for mosses, lichens, grasses, sedges and heaths, the layer communities are shuffled back and forth like a deck of cards. Each stand is just another deal. The layer (union) seems to be a better unit than the local juxtaposition of layers.*

All that has been discovered about the structure, composition and distribution of synusiae is true and profitable. But it is not yet proven that synusiae are universally of prime importance. For in theory the layers are always interdependent. And in middle and lower latitudes and altitudes the interdependence has been proven. Certainly the layers are always important, and are useful indicators of site-quality.

Faegri (1937) sums up the relation of the Zürich-Montpellier and Scandinavian Schools thus:

> In the rich and varied flora of middle Europe the association is a handy instrument of research, giving a general view of the ecologic relationships without losing itself in less important particulars; in the poorer vegetation of northern Europe the sociation is that instrument of research by the aid of which one can penetrate deeply into the ecology even of a floristically very monotonous and poor district.

The Danish School

In closely settled, homogeneous little Denmark statistical studies have prevailed under the influence of Raunkiaer. Classifying all plants into groups according to the way in which the plant meets its most unfavorable season, Raunkiaer divides the species of the world into "life-forms": Phanerophytes, Cryptophytes, Therophytes, etc. The percentage of species in each group in a very large list of species drawn from all over the earth gives the "normal

* Lippmaa (1935) has used the unions to great advantage in describing the vegetation of the island of Abro.

spectrum" for the earth as a whole. Similarly the percentages in the flora of any given region form a spectrum for the region. A region with a much larger than normal percentage of Hemicryptophytes or Therophytes, for example, has a Hemicryptophyte — or Therophyte — flora and climate. This scheme has been widely used. In association tables of the Zürich-Montpellier School it is customary to precede each species name with the initial of its life-form. The spectrum of an Association, Alliance or Order is a very useful datum.

One difficulty with the Raunkiaer life-forms has been that botanists do not always agree upon the life-form to which a species should be attributed. A very critical study of this matter by McDonald (1937) should remove this difficulty, so far as the flora of the northeastern United States is concerned. But it must be conceded that some species winter differently in different climates, i.e., belong to different life-forms, and still are able to increase and multiply.

In this country it has been customary to study the vegetation of political units: a county or a State, as Raunkiaer apparently did. The resulting spectra are not very illuminating. It is found, for example, that the spectra of Mississippi, Alabama, Connecticut, Long Island, Indiana, and Iowa are practically alike. Cape Breton and the Olympic Peninsula are similarly overweighted with Hemicryptophytes (McDonald, 1937). Thus all of these areas have a "Hemicryptophyte climate"! The expression is valueless, if not deceptive.

Such an absurdity is due in part to the use of political units instead of biotic areas. In Iowa there is enough of mesic forest to contain most of the species found in Indiana or Connecticut. But if we compare the spectrum of the prairie with that of the oak-chestnut forest, the difference between Iowa and Connecticut would be evident. The spectra of associations are very suggestive.

Jones (1936) has used the spectra of the Merriam Life Zones very interestingly, showing their relation to certain other circumscribed areas. Thus the Arctic-alpine zone of the Olympic Mountains (Wash.) has about the same spectrum as Spitzbergen or St. Lawrence Island. The Transition zone is similar to Connecticut and Central Switzerland. This latter conclusion is surprising, seeing that the Olympic forest is in the heart of the Pacific Conifers, and Connecticut is largely Oak-hickory. Unfortunately the Raunkiaer scheme does not distinguish between conifers and broadleaf trees; all are megaphanerophytes. Nor, of course, does it distinguish between a winter-wet and summer-dry climate (Olympic) and one with adequate moisture throughout the year (Connecticut).

Raunkiaer's calculations of the percentage of pteridophytes, mosses and liverworts in a Flora are most illuminating. But it would seem that here also one needs to know something about the *quantity* of each species. At least the use of political units is a source of error. In Iowa several boreal mosses are found in only one or a few localities, all in the northeastern eighth of the State. They are excellent indicators of microclimates, but wholly deceptive with regard to the climate of Iowa (Conard 1938). Yet in a "list of species" or a Raunkiaer spectrum or quotient the rarest moss, e.g., *Seligeria pusilla*,

looms just as large as *Brachythecium oxycladon* that covers acres all over the State.

The Russian School

As summarized by Sukatchew (1934) Russian phytosociologists were primarily interested in the Steppe vegetation and its relation to forest. Their work is directly applicable to our central United States. The Russians were the first to recognize the relation of soils to vegetation and climate (Glinka 1914). It is most regrettable that so much of their work is inaccessible to other peoples because of the barrier of language. Sukatchew regards the phytocoenose as the fundamental unit of plant sociology — a unit characterized by the species-list, the structure and arrangement of the synusiae, the physiognomy, and the biological effects of the complex of habitat-factors. Coenoses which are alike in these respects compose a phytocoenose-type or Plant Association.

The Chicago School

In North America Cowles and Clements have exerted a dominant influence. With them the prime object of the study of vegetation is the elucidation of the causes and processes of vegetational change: Succession. A visit to Cowles's favorite sand dunes on Lake Michigan clarifies his viewpoint. Shores and sand dunes are truly marginal lands, because of great instability of the substratum and lack of moisture and nutritive salts. The relation of vegetation to physiographic change is conspicuous because of the rapid changes of both. The moving sand cuts your face and salts your luncheon. Within a mile one can see every step in the building and removal of dunes, and the establishment of mesic forest. The sand becomes a soil by incorporation of humus. Evaporation is reduced by the presence of pioneer plants and mesic microclimates develop from xeric.

Cowles busied himself with working out the consequences of succession and physiographic change and teaching these large ideas to his pupils. His plant-geography was general, based upon species rather than upon communities. As an example may be cited his listings of intraneous and extraneous species. In his association lists abundance was indicated only by the order in which the species were named. Thus the association as now defined was scarcely recognized.

Cowles's pupils outdid their master in finding evidences of succession everywhere. No paper was complete without at least an imaginary sequence of "associes." It would be invidious to cite examples.

The Nebraska School

Clements did his earlier work in another type of marginal land, the climatically arid. The tallgrass prairie of eastern Nebraska is threaded through with galeria forests along the major streams, and merges westward into the shortgrass plains. The prairie presents vast stretches, scores of miles, of dense grass sod. In June *Stipa spartea,* with decimeter long awns and two foot

stems, nods in the persistent breezes. The stalks of *Andropogon scoparius* reach a height of three feet in August. Amidst this a wealth of showy composites blossoms. On drier banks the grasses are shorter and thinner, and red and purple mallows add color. Wet prairie is a waving mass of *Spartina Michauxiana,* up to six feet tall, with *Helianthus* spp., *Silphium* spp., and abundant Asters. The prairie is so extensive, the spreading forbs so scattered and conspicuous, the isolated annual and perennial herbs so disperse (Chapman 1936), as to make it nearly impossible to delimit stands or define associations. It is the Prairie.

On the margins of wet places and woods the struggle for existence is intense. Seasonal fluctuations of climatic factors are numerically great, and proportionately excessive. For this is marginal land. The average rainfall is too low for tree growth. The actual extremes, 14 in. to 30 in. in one locality, run from aridity to abundance.

In the Sandhills of northwestern Nebraska we have a hundred miles of shifting sands. No tree exists, excepting a few scrubby Celtis in the shelter of a hill, or some cottonwoods along a stream. Hundreds of shallow ponds occupy the hollows of the hills, usually without outlet or inlet. Around these are rings of vegetation, surging back and forth with the seasons. In September 1937 I found large mats of the aquatic moss *Drepanocladus aduncus polycarpus,* dead and old, on low hayland half a mile from a shrunken lake.

The sandhills rise as much as 200 ft. above the lake beds — an endless maze of mighty inland dunes. Always the white sand is conspicuous, amongst creamy Mentzelias, beds of pink "Stevia" (Othake), Tradescantia, and countless Chenopodiums and low Helianthuses. *Yucca glauca* tufts the drier hills. And at intervals the wind cuts into the sand, blows out a hole as big as a house, and vegetation begins anew its stabilizing role: a blowout.

On this background Clements developed his insistence on succession and the climax, and his extensive terminology — "bewundert viel und viel gescholten." No wonder zonation looms large, and is a sign of succession. It *is,* in such a place. No wonder the association was not recognized as it was in central Europe, or the layer (union) as in Scandanavia.

The studies of Weaver and his colleagues have given us very minute descriptions of prairie vegetation and the prairie habitat. Including his records of roots, and the studies of grazing problems by many investigators, probably no type of vegetation has been so minutely described as has the prairie. Recently the phenomena have been successfully described in terms of the association by Steiger and by Hanson.

Nothing can be gained by questioning the validity of the phenomena that have been noted by the various workers in plant ecology. Much of the work has been done well. Nor need we question the value of the concepts arrived at by the leaders of our science. But a very great advantage would accrue if we could find a best method for the study, and especially the description of vegetation. At least, an internationally accepted terminology would help. At present the terms Association, Union, Alliance and Order have international standing. And the Association is defined by its characteristic combination of

species, i.e., by the species present, and the role of each species. For a dominant species in one association may occur as an accidental in another. Thus a mere list of species is of extremely little value. The old lists "in the order of their abundance" are scarcely better. It is important to know all of the analytic and synthetic details indicated in recent guides (Braun-Blanquet 1932; Reynaud-Beauverie 1936). We may now proceed to examine the associations that are known and have been described. Only so can we determine the value of the Association concept, and the extent to which it can be profitably applied.

Plant Communities on Land

Land plants, as distinguished from those of air or water, have a permanence of location that makes them live in communities willy nilly. Some of these cases of proximity are certainly fortuitous. In most cases relations of dependence supervene, and a definite social relation develops. The community acquires a more or less definite composition which is repeated in many stands. Thus both by observation and by mathematical analysis the Association has been shown to be a biological entity and not a mere chance gathering of plants. When the associated animals are considered, the biocoenose becomes an indubitable social unit.

The most complete list of categories for plant communities is that of Rübel as recently extended and completed (1930, 1936). The list smacks somewhat of the arm-chair and one is led to question whether natural vegetation is susceptible of such an orderly and repetitive classification. But Rübel is probably the most widely traveled and most critically objective ecologist the world has produced and certainly no one is better qualified to prepare an outline of the Plant Associations of the Earth. And he accompanies his categories with concrete examples in a most convincing manner. It would be interesting to know whether a sample association in each of Rübel's categories has been carefully studied. So far as I know such sample studies are not available. To make them would be a worthy project for some foundation.

In the following pages we have attempted to summarize some samples of communities of land plants, aranged in the order of their sociological complexity, beginning with the simplest.

One Layered Communities

The simplest communities of photosynthetic land plants are made up of one species of alga, e.g., a film of Protococcus (Pleurococcus) on board, brick or bark; a film of Trentepohlia; a sheet of Gloeocapsa. The "Protococcetum" is a layer of globular and colonial unicells, the "Trentepohlietum" a velvet of short threads. There is no social relation beyond the family relation of the cells or filaments, and some competition for position. In mild or warm temperate climates these algae require partial shade. The shade of a rock or wall is as good as the shade of a tree, provided the moisture conditions are adequate. In the town of Grinnell, Iowa, the north side of certain elm *(Ulmus americana)* trunks with a diameter of 3 or 4 feet bears heavy films of Protococcus. No other species of tree (out of about 50) is so favorable in this

locality. It is not so in other parts of the United States. Protococcus has no predilection for elm bark except in the type of climate found in Grinnell, Iowa, (and of course as far as that type of climate extends. Perhaps a study of the preference of Protococcus for elm bark would reveal the geographic range of this type of climate — a kind of summation of atmospheric climatic factors). Reference may be made here to epi-endolithic alga communities of southern Tyrol (Braun-Blanquet, 1932, p. 188; Diels 1914).

Extremely simple associations of bacteria and lichens inhabit exposed rocks, at least in temperate and colder zones and at high altitudes. Some of these plants actually penetrate the rock. Others are merely attached to it. Some species are confined to calcareous rocks, some to crystalline, some flourish on both. Fink (1895) found in Iowa 32 species of lichens on calcareous rocks, 17 on granite, 4 on both, 4 on sandstone.

Nordhagen mentions Gyrophoreta in the Sylene National Park of Norway. Some vertical rock walls at 800-1000 m. are covered with beautiful stands of *Gyrophora leiocarpa*. A *Ramalina polymorpha* association is found on rocks frequented by birds (ornithocoprophile lichen-association). E.g.:

Ramalina polymorpha	5
Xanthoria lychnea	2
Gyrophora arctica	1
Alectoria jubata	2
Prasiola sp.	2

A similar association consists of

Gyrophora arctica	5
Ramalina polymorpha	1
Xanthoria lychnea	1
Parmelia saxatilis	1
Cynodontium strumiferum	1

In the Tatra (Motyka 1926 quoted by Braun-Blanquet 1932, p. 241) bird-roost-rocks carry the extremely nitrophilous Ramalinetum strepsilis:

Ramalina strepsilis
Rinodina demissa
Xanthoria fallax
Physcia tribacia

But the association changes with the slope of the rock, a single boulder having on top Ramalinetum strepsilis; on the sloping side Alectorietum chalybeiformis *(A. chalybeiformis, Gyrophora cirrhosa, Lecanora frustulosa, L. melanophthalma)* and on the vertical sides the Gyrophoretum cylindraceae (with *Cetraria noermoerica)*. Thus our lists of the lichens drawn up by the systematists signify little about lichen communities. Even Fink's (1904) description of a lichen society of a sandstone riprap cannot be used as an outline of lichen associations.

On freshly exposed soil in the eastern United States *Baeomyces roseus* often covers many square yards of sloping banks (newly graded cuts for roadways). This distinct association, often with *Pogonatum brevicaule*, is common about Philadelphia, Penna., and on western Long Island. It has not been studied sociologically. The surface soil is firmly held by the mycelium, after

the manner of the rhizoids of a moss. To the Bryophyte communities we now proceed.

Two Layered Communities: Moss Communities

The mosses always yield a more complex community because they have rhizoids. Many moss communities have been described both in Europe and America. They are at most two layered communities of low stature — a shallow layer in the substratum (rhizoids or underground stems) and the aerial layer. I am not aware of any case where a "tall" moss habitually is accompanied by lower species, although one might expect as much from Dawsonia.

Perhaps the simplest bryophytic community is that described by Griggs (1933, 1936) on the ash of Katmai in Alaska. *Cephaloziella byssacea* covered extensive areas 18 years after the eruption. In culture it proved to be able to grow on a nitrogen-free medium. *Lophozia bicrenata* was often associated with Cephaloziella but was unable to grow on the nitrogen-free medium.

In the Alps and in Scandinavia an association of Anthelia is well known. Nordhagen (1928) found it on places wet with snow water, and with a very short growing season. The association includes:

A. Juratzkana
Cesia varians
Cephalozia ambigua
bicuspidata
Cephaloziella Hampeana
Lophozia alpestris
incisa f. *alpina*
Floerkii
ventricosa
Moerkia Blyttii
Nardia Breidleri
Pleuroclada albescens
Conostomum boreale
Dicranum falcatum
Starkei
Oligotrichum incurvum
Polytrichum alpinum septentrionale
piliferum
sexangulare

Apparently these represent three associations, the areas with shortest season being occupied by liverworts. Dicraneta and Polytricheta require a longer growing season.

Snowland wet with cold spring water (Nordhagen, 1928) bears great cushions of *Pohlia glacialis*. In warmer water is a carpet of *Pohlia commutata, P. Ludwigii* and *Bryum Duvalii*. Sometimes a wet depression is covered with *Drepanocladus purpurascens*. In all of these associations there is usually no vascular plant.

Polytrichetum sexangularis has been described by Szafer from the Tatra and by Braun-Blanquet from the Alps, at 2500-2900 m. It occupies soils of maximum acidity, preferably in stagnant water (hochalpiner Sumpf). Frey says this association is adapted to a very long snow cover; the snow does not melt away every summer. Of three high-alpine associations Anthelietum has the smallest requirement for warmth and vegetative period, and the highest water requirement. Salicetum herbaceae requires the least water and the longest vegetative period. Polytrichetum takes a middle position.

Rhacomitrium lanuginosum association is recorded for the Auvergne, on basalt rubble, at 1100 m. The top of Knocknarea, 1000 ft., at Sligo, Ireland, is covered with tufts of this moss. Heathers and other small plants are abundant but not conspicuous. *Rhacomitrium ramulosum* forms an association on

certain steep exposed rock faces in western North Carolina (Oosting & Anderson 1937).

Many "moss associations" and "lichen associations" have been described as living only under the shadow of larger plants. It seems more consistent to regard these as layers in associations of larger plants. The term "union" used by Lippmaa, Cain et al. for the moss layers is preferred. And if moss unions of definite floristic composition are found to occur in various "associations," we shall have made progress toward a better understanding of Vegetation.

Simple Associations of Vascular Plants

Simple associations of vascular plants with one exposed layer are numerous. They are more complex than one-layered moss communities because the root layer is more extensive and has more adjustments than has the rhizoid layer of a moss community. The interaction of roots is still but little understood, although Loehwing (1937) gives a bibliography of 422 titles on the subject. There is a wealth of material on these simpler associations of vascular plants. Mention may be made of

Salicornietum ambiguae	Ammophiletalia mediterranea
Spergularia-Plantago-decipiens association	Salicornietalia mediterranea
Suaedetum maritimae	Asplenietalia rupestris
Andropogonetum scoparii	Isoetetalia

among open associations, and the closed associations of

Ruterto-Secalinetales	many grass and sedge associations
Andropogonetum Hempstedi	Lawns, pastures and haylands.
many marsh associations	

As an example of an open simple association we select, more or less at random the Association of Suaeda maritima and Kochia hirsuta (Braun-Blanquet 1933)

Characteristic species:

IV *Kochia hirsuta*	IV *Salicornia herbacea* ssp. *Emerici*
I *Cressa cretica*	

Characteristics of the Alliance (Thero-Salicornion)

V *Suaeda maritima*	III Atriplex hastata triangularis
V *Salicornia herbacea* ssp. *patula*	II Salsola soda

Characteristic of the Order (Salicornietalia)

I Obione portulacoides

Synecology.—This association, often discontinuous (coverage 60-80%), selects a soil high in salt (NaCl) content, marly, formed in part of shells accumulated on the borders of ponds. It is an unstable grouping of therophytes, changing from year to year. Several facies are distinguished according to the predominance of Kochia, Suaeda or Salicornia.

Of closed one-layered associations perfect examples are found in Distichlidetum and Spartinetum. Spartinetum patentis appears in two facies, one dominated by *Sp. patens* and one by *Juncus Gerardi.* It covers acres or miles

of level marshland along protected bays of the Atlantic and Gulf coasts from Nova Scotia to Louisiana and Texas. Within this extreme range of climate the required conditions are a fine silty soil rich in humus, submergence in sea- or brackish-water at least at spring tides, a flat plain at about the level of mean high tide, and freedom from erosion. The composition of this association at Cold Spring Harbor has been described thus (Conard 1935):

	Ab.	C.E.	Vt.	Soc.	Constr.	Notes
Spartina patens	5	5	4	5	123	
Juncus Gerardi	3	3	3	3	23	
Limonium carolinianum	1	+	4	1	4	
Pluchea camphorata	1	+	4	1	4	
Distichlis spicata	1	+	3	3	5	leading to Distichlidetum
Iva oraria	1	+	3	1	5	leading to shrub association.

Max Moor (1936) has presented in the Isoetetalia the beginnings of the two-layered community. In some of the communities of the Nanocyperion there is no competition either of roots or tops. But the species are similar in life-form and manner of growth, in their rapid development and short duration, in the main outlines of floral ecology, and in distribution.

Mosses and algae form the ground layer, flowering plants the herb layer. But all of the plants are so small (85% of them not over 5 cm. tall) that mosses and phanerogams form a united sod in which layering is scarcely perceptible.

Eleocharetum ovatae, a community of the margins of ponds, is credited with 20 characteristic species of the association, including

Eleocharis ovata atropurpurea — *Physcomitrella patens*
Marsilia quadrifolia — *Riccia crystallina*

Characteristics of the Alliance 13, including

Gnaphalium uliginosum — *Riccia glauca*
Plantago intermedia — *Archidium phascoides*
Gypsophila muralis

Characteristics of the Order 6, including

Juncus bufonius — *Myosurus minimus*
Lythrum hyssopifolium — *Riccia sorocarpa*

Differential and companion species 16, including

Bidens cernuus radiatus — *Veronica scutellata*
Chenopodium rubrum humile — *Alisma plantago-aquatica terrestris*
Eleocharis acicularis — *Polygonum hydropiper*
Ranunculus flammula — *Riccia fluitans*

One feature of this association is the sporadic appearance of many of the species. Absent over large areas, and often lacking for years, a species may suddenly reappear in certain places and seasons in unlimited abundance.

The Eleocharetum ovatae lives its life in two months, owing to fluctuations of water level. In this period may be seen two facies: 1, Riccia and other cryptogams; 2, the phanerogams.

The substratum is an impervious layer of glacial or loessial loam overlaid

with 1 or a few cm. of mud. This layer is highly nitrogenous, and retentive of water. The slope must not rise more than 50 cm. at 20 to 40 m. from the margin of the water, in order to maintain an adequate water supply; pH 4.8-5.5.

Dissemination of the species, succession and geographic distribution of Eleocharetum ovatae are fully discussed by Moor. The whole story is constantly suggestive of associations seen in North America.

Grasslands

Grasslands are generally found to be two or three layered above ground. Weaver, Hanson and Pavlyschenko have shown rootlayering under ground. Albertson (1937) found in west central Kansas "three general types of vegetation with varying degrees of intermixture"*:

The short-grass (Bulbilis-Bouteloua) type
Little Bluestem (Andropogon scoparius) type
Big Bluestem (Andropogon furcatus) type.

The Bulbilis-Bouteloua type has two dominant species *(Bouteloua gracilis, Bulbilis dactyloides),* 6 "principal species of grasses and sedges," including *Agropyron Smithii* and *Andropogon scoparius;* 8 "grasses of secondary importance," including *Andropogon furcatus, Distichlis stricta, Hordeum pusillum* and *Sporobolus asper;* 27 "principal species of forbs," including *Ambrosia psilostachya, Aster multiflorus, Grindelia squarrosa, Ratibida columnaris* and *Solidago glaberrima;* 32 "forbs of secondary importance," including *Acerates viridiflora, Achillea millefolium, Draba caroliniana, Lygodesmia juncea, Oxalis stricta* and *Verbena bracteosa.* Figure 22 shows three heights of shoots in this community and two types (and depths) of root systems. Thus a five layered structure may be stated for the short-grass association. Albertson gives extensive data on the habitat, and shows by maps of permanent quadrats the effects of the great drought of 1934. The "types" above are apparently associations in the international sense.

Relations of competition of tops and roots of grassland plants are often discussed. Relations of dependence are rarely mentioned. It seems certain that several of the species depend for survival upon the fact that the ground is shaded by the mass of vegetation. Soil temperatures are thus kept low. The large amount of humus in the soil is due especially to the grasses. And this humus is essential in regulating the water of the soil, and therefore in the survival of many grassland species. Prairie soils degenerate rapidly under trees, becoming pale and clayey. Leguminous plants abound in the prairie. It is often said that they are important to the association (constructive) in the gathering of nitrogen. They do possess root-tubercles. I am not aware of any measurement of their contribution, or of any attempt to eradicate the legumes and see the effect.

Andropogonetum Hempsteadi of western Long Island has been critically studied by Cain et al. (1937) from the sociological standpoint. Floristically

* Albertson follows Clements in considering the prairie "a distinct plant association."

and ecologically it shows a remarkable similarity to the Andropogoneta of the midwestern prairie, of which exact sociological studies have not yet been published. The occurrence of these associations in such diverse climates is due to differences in soil. The pervious gravel of Long Island with 40 in. of annual precipitation supplies water to plants about as well as does the fiine loessial soil of the middle west with 25 to 30 in. of precipitation, and a low humidity.

The prairie of western Iowa and eastern Nebraska has been floristically described by Weaver and Fitzpatrick. However, these authors do not recognize "associations" in the international sense, and it is impossible to construct association tables from their admirable description. Six associations are indicated in their six major communities:

Andropogon furcatus community	Stipa spartea community
Spartina Michauxiana community	Sporobolus heterolepis community
Andropogon scoparius community	Panicum-Elymus community

Hanson & Whitman found in North Dakota

1. Bouteloua gracilis-Stipa comata-Carex community
2. Agropyron Smithii-Bouteloua gracilis-Carex filifolia community
3. Andropogon scoparius community
4. Calamovilfa longifolia community
5. Artemisia cana community
6. Distichlis stricta-Agropyron Smithii community
7. Distichlis stricta-Puccinellia nuttalliana community
8. Buchloe dactyloides community
9. Andropogon furcatus community

Apparently these communities deserve the rank of associations in the international sense. The paper gives the floristic composition of each community, topography, soil profile, soil texture, concentration of soluble salts, soil reaction and other environmental factors.

From the several papers mentioned above it is clear that there are a number of Andropogoneta, making up an Andropogonion of wide distribution and great interest. Clements and Clements (1933) state that the apparent dominance of Andropogons is due to disturbance. The degree of dominance of *Poa pratensis,* Andropogon and Sporobolus serves as "an index to the period of human occupation," "and the corresponding pressure on the original prairie."

The literature on ecology of grassland is summarized by Hanson (1938), with a bibliography of 117 titles. To this should be added the papers on Andropogonetum scoparii by Blizzard (1931) and Olmstead (1937). European studies of grassland are only lightly touched by Hanson.

Bharucha (1932) has given a detailed sociological study of a grassland community in the vicinity of Montpellier, France: The Association of Brachypodium ramosum and Phlomis lychnitis. The soil is brownish or reddish (terra rossa). It is alkaline and contains an abundance of soluble salts, owing to upward movement of water in the dry summer season. It is very low in humus, because of the presence of lime, and the arid summers. Moisture and low temperature in winter favor active hydrolysis of the sesquioxide of iron

and the silica of the soil. Rain falls in spring and autumn; summer is practically rainless. Evaporation is lowest in winter. Summer temperature rises daily to 30 or 35° C; mean temperature in winter is 6.9° C, but about once in ten years a minimum of -12° C is known. Total precipitation is 754 mm., with 106 rainy days. Humidity 75% in winter, 56% in summer. Snow falls but rarely, not every year, and does not affect vegetation. Freezing temperature sometimes injures *Medicago* spp., young shoots of *Quercus ilex* and a few other species.

The association of Brachypodium ramosum and Phlomis lychnitis is the result of degeneration of Quercetum ilicis, due to clearing, repeated burning over, and intensive pasturing by sheep and goats. It may further degenerate into a thorn-scrub with *Euphorbia niceensis* and *E. Characia*. 111 species are listed in 22 typical stands and 10 variants. 75 other species were seen from 1 to 4 times. Three mosses and 6 lichens are listed. Exclusive, preferential and differential species are indicated, as well as characteristics of the alliance, and companion species. A vast amount of other data fills the pages of Bharucha's paper.

A summary of certain pasture-associations of central Europe is given in Prodromus der Pflanzengesellschaften Fasz. 5, Verband des Bromion erecti, by Braun-Blanquet & Moor (1938). The Brometalia erecti are treeless or nearly treeless grasslands of level ground, where the soil becomes very dry in summer, and the grass is either pastured or mowed, but not manured. They occur in France, Holland, Great Britain, Germany, Switzerland, Austria, Italy and Dalmatia. Bromion erecti included 29 associations and subassociations, in three suballiances. Four related associations are described in a series of appendices.

A rich and nearly untouched field for the plant sociologist is that of the associations of cultivated grounds. Braun-Blanquet has made a start with his Ruderecto-Secalinetalia (1936a). Conard (1935) mentions a Portulacetum. The cultivated plants and their accompanying weeds often form communities that are repeated annually in countless stands. Ruderal communities on new or abandoned land often show definite composition and sequences (Thone 1915, 1916). Permanent pastures and haylands have been extensively studied in Europe. Critical sociological studies of gardens, lawns and agricultural lands are greatly needed. For from them should follow a more exact knowledge of weed control and increased production.

The Desert

In deserts the lack of water is by far the most impressive factor. The responses of plants are such as to give to all deserts a similar physiognomy. Says Henslow (1894):

> On first entering the desert near Cairo (Egypt), where plants are to be found—namely, along the water courses, which are dry all the year round excepting in February and March, while no plants occur on the higher ground at all—the general appearance is of low shrubs or isolated tufts of a nearly uniform grey color. The plants are never crowded or cover the ground like an English roadside. In other words, they do not struggle for an existence with one another, but only with their inhospitable inorganic

environment. The grey color is mainly due to intense hairiness, which subdues the green hue of chlorophyl. * * * The next obvious feature is the stunted character of the bushes, three feet being about the maximum height (Zilla mayagroides), with gnarled stems at base. This is often coupled with a spinescent character, either in the branches (Zilla), foliage (Echinops), or stipules (Fagonia) and bracts (Centaurea).

It has since been shown that there is root competition amongst desert plants, even when the plants are "isolated" and do not "cover the ground like an English roadside." Cannon (1911) found two types or root system: 1, superficial, near the surface of the ground, horizontally extensive, and subject to considerable adjustment of position and extent. 2, deep, reaching to deep sources of water, with but little capacity for adjustment.

For over thirty years exact studies of the desert environment and vegetation have emanated from the Desert Laboratory of the Carnegie Institution of Washington at Tucson, Arizona. MacDougal, Clements and Shreve have been the principal contributors. In 1936 Shreve published an outline map of the desert areas of North America. The following year Shreve & Hinckley (1937) reported "thirty years of change in desert vegetation." A plot 100 m. square on the domain of the Laboratory, with shallow soil strewn with basaltic rocks, had the following total populations of plants above the hemicryptophytic level:

	in 1906	in 1936
Carnegiea gigantea	2	1
Cercidium microphyllum	2	5
Fouquieria splendens	1	0
Lycium berlandieri	10	11
Janusia gracilis	6	17
Jatropha cardiophylla	1	4
Encelia farinosa	80	146
Lippia wrightii (1 in 1928)	0	0
Menodora scabra	0	1
Verbena goodingii nepetifolia	3	0
Franseria deltoides	0	1
Haplophyton cimicidium	0	2
Abutilon crispum	17	0
Sphaeralcea grossulariaefolia pedata	1	3
Abutilon incanum	4	0
Brickellia coulteri	0	2
Notholaena hookeri	9	0
Total	136	193

Shreve & Hinckley explain that phanerophytes were used because they could be mapped and counted in the dry season "in order to avoid the heavy growth of annuals which makes the visibility of the small perennials poor."

Coville & MacDougall (1903) state, p. 12,

The woody vegetation in the vicinity of Tucson consists chiefly of creosote bush (Covillea tridentata) interspersed with several species of Opuntia, most of them with cylindrical stems, and occasional plants of joint pine (Ephedra trifurca) and barrel cactus (Echinocactus), with an abundance of mesquite (Prosopis) and cat's claw (Acacia greggii) in the lower drainage areas. Upon the foothills occur in addition the giant cereus (Cereus giganteus), two species of palo verde (Parkinsonia micropylla

and P. torreyana), ocotillo (Fouquieria splendens), two species of Lycium and many other woody plants. This is of course in addition to a great variety of annual vegetation which may spring up between the sparse shrubs after any drenching rain, particularly the slow rains of winter.

Thornber (1909) has listed all of the plants then known to him in the vicinity of the Desert Laboratory under the following captions:

I. Tumamoc Hill: trees, shrubs, woody climbers, dwarf shrubs, half-shrubs, perennial herbs, biennial herbs, annual herbs (winter annuals, summer annuals).
II. Mesa-like mountain slopes: divided as above.
III. Santa Cruz flood-plain; divided as above, with also miscellaneous introduced species.

We are left without associational groupings and without any estimate of the quantity or the role of each species. The environmental factors have been extensively studied by the workers at the Laboratory. Physiological studies of the native plants have also been numerous.

All of these reports emphasize the well known fact that in making adequate sociological studies in the desert it is necessary to use permanent quadrats. These must be examined at various seasons, and in a number of years, because of the extreme variability of the climate. Mean rainfall at Phoenix, Arizona, is about 5 in. But in 1905 that station recorded 19.7 in. It would take seven years with only 3 in., or 3 years with none at all, to bring the average down to 5. The differences in vegetation, therefore, from one year to another are extreme.

Sociological studies of the vegetation of the northwestern Sahara have been published by Maire (1924, 1925, 1928).

Low Tree Associations

A low tree association, Quercetum ilicis, of the Mediterranean Garigue has been minutely described by Braun-Blanquet (1936). The stands range from 5 to 55 m, above sea level, in France, Spain, Italy and Morocco. The trees range in height from 3 to 20 m., with covergrades from 80 to 100%. The inferior strata cover from 5 to 90%. Characteristic species, characteristics of the Alliance and Order, companion species and mosses are tabulated. Of the mosses listed *Hypnum cupressiforme, Scleropodium purum, Brachythecium rutabulum, Fissidens taxifolius* and *F. incurvus* are familiar; *Eurhynchium circinnatum* is one of the rare mosses of Killarney in Ireland, where *Arbutus Unedo* and other Mediterranean species are found.

Quercetum ilicis is a low, open forest of slender, crooked and leaning evergreen oaks, usually 8 to 12 m. tall. Mixed with the holly oak are generally *Quercus pubescens* and *Acer monspessulanum*. A lower tree layer includes *Phillyrea media* and *Arbutus Unedo*. An upper shrub layer includes *Viburnum tinus, Rhamnus alaternus* and *Pistacia lentiscus*, all with evergreen leaves. *Quercus coccifera* is very much reduced by the shade, but is always ready to take a leading place when *Q. ilex* is cut off. A lower shrub layer is characterized by the abundance of *Ruscus aculeatus*. The low herb layer, made up of herbs and mosses rarely covering more than 30% of the ground, is feebly developed.

Occasionally *Hedera helix*, creeping on the ground, covers large areas. 19 agarics and 1 polypore are listed. Each stratum is dependent upon the others.

Under the caption "Associations Dépendantes" Braun-Blanquet cites Fabronietum pusillae, a moss community on the shaded trunks of old trees, and Parmelietum trichoterae, a lichen community of the branches of old trees.

Using these findings as a text, Braun-Blanquet remarks: (p. 54)

Nous avons vu que l'association bien développée du Quercetum ilicis galloprovincialis constitue une unité biologique harmonieuse et très sensible aux interventions de l'homme.

Si la strate arborescente, créative, conditionne tous les autres strates, y compris les associations d'epiphytes dépendantes, chaque state concourt au bon fonctionnement de l'ensemble et au maintien des conditions ambiantes indispensables à la régénération perpétuelle de la forêt climatique.

P. 28,

Voilà pourquoi nous ne pouvons admettre l'opinion de certains auteurs qui confèrent à *chaque strate* d'une forêt la valeur *d'une association* spéciale et autonome.

Exactly for this reason the use of the term "association" for the dependent communities of mosses and lichens seems unfortunate. Cain & Sharp (1938) have found moss communities of definite composition and with definite environmental requirements which they call "unions." Each union is characteristic of one or a few tree-associations. Billings & Drew (1938) have shown the relation of moss unions on trees to certain species of tree. The water-holding qualities and chemical nature (pH) of the bark are the important factors.

In discussing soils Braun-Blanquet remarks (p. 84):

Dans les contrées humides et tempérée-froides, l'action des facteurs biotique est prépondérante dans l'édification du profil. * * * Plus on approche des pays arides et plus le rôle des organismes dans la formation du sol s'affaiblit pour devenir négligeable dans les contrées désertiques ou l'influence des facteurs anorganiques * * seule se manifeste.

P. 85,

D'une façon générale, on peut dire que chaque association végétale (chez les associations forestières même chaque faciès), a son profil de sol particulier.

The soil profile, therefore, changes as the vegetation changes, and a mature or climax soil accompanies a climax association. The two do not develop wholly contemporaneously. The plant climax may appear many years in advance of the soil climax. P. 83,

Tandis que l'évolution du profil climatique se poursuit assez rapidement dans les conditions et sur un substratum favorable (un profil de Podzol peut se former en moins de 1,000 ans), la maturation est infiniment plus lent dans d'autres conditions.

Some rocks may never give rise to a climax soil.

The dependence of soil upon the mineral substratum on the one hand, and on vegetation on the other, has been clearly set forth by Watt in England and by Tüxen in Germany. These workers also recognize differences of soil profile under different facies of an association. Svinhufvud (1937) found significant differences in the soils of Cajander's forest types, thus corroborating the conclusions of Cajander based upon the low vegetation. The differences were in microflora (bacteria and fungi), in available P, K and NO_3, in nitrifi-

cation and dentrification. These are primaily due to differences in the content of water and humus. Friedel (1938) has followed soil development below the Rhone glacier, where the dates when the ice retreated from each area are known. Brownearth is developed where there was ice in 1602 A.D. Podsols are found only where the ice retreated before, mostly very long before, that date. Alway et al. (1933) found four kinds of forest "on the same soil type," a uniform sandy soil on Star Island, Cass Lake, Minn. The only differences they found were in the character and acidity of the duff and leafmold. It is possible that significant differences would be found by the methods used by Watt and Tüxen. Certain it is that "soil type" according to the United States Bureau of Soils has little relation to the soil classes of Glinka and his followers. Heimburger (1933) however found that similar types and similar stands may occur on very different soils. These disagreements need clarification.

Quercetum galloprovinciale occurs upon a great variety of mineral substrata: on soft or on crystalline lime rocks, on dolomite, on basalt, gneiss and granite, on pliocene and recent alluvium. The developed soil is in every case a true terra rossa. There is accumulation of iron and aluminum in the B-horizon. SiO_2 is still abundant (54-68%).

High Forest

The forests studied by Watt and Tüxen must be classed as "high forest." They have sociological structure closely paralleling that of Quercetum ilicis. Perhaps the most extensive study of such forest is to be found in Die Buchenwälder Europas, edited by Rübel (1932).

Coniferous Forest

Coniferous high forest has been minutely studied in Finland, whence comes the work of Cajander and his colleagues. Ilvessalo has reported in similar manner the northern coniferous forests of North America. Heimburger has carried this work still further.

Coniferous forests in general have very meager understories. The herb layer and moss layer are best represented, with sometimes a low shrub layer. Hult and Sernander have developed a square chart which sharply visualizes the layering in forests. Jones (1936) states for the Olympic Peninsula of Washington (p. 32) "The forests of the Douglas fir-hemlock association are characteristically dense and dark. The humus content of the soil is usually thin, except for decaying wood. Because of its inability to reproduce under heavy shade, there are few or no young Douglas firs in these forests. The chief shrubs are" *Gaultheria shallon, Berberis nervosa, Vaccinium parvifolium, Salix scouleriana.* The most abundant ferns are *Pteridium aquilinum lanuginosum, Polystichum munitum* and *Struthiopteris spicant.* The Tsuga heterophylla-Thuja plicata climax forest is the chief association of the Olympic Peninsula. "The general character of the climax forest is dense, somber and mossy, consisting often of nearly pure stands of straight slender hemlocks." "The forest floor is carpeted with thick growths of Eurhynchium Oreganum, Hylocomium loreum, H. triquetrum" and other mosses. The under-

growth is sparse: *Vaccinium parvifolium, V. ovatum, Menziesia ferruginea, Pachystima myrsinites, Oplopanax horridum, Gaultheria Shallon, Rosa gymnocarpa, Ribes bracteosum,* etc.

The need and the promise of sociological studies in the northern coniferous forests of North America may be emphasized by a comparison of the forest site-types recognized in that area by Ilvessalo and by Heimburger.

Ilvessalo's types	Heimburger's types
Arctostaphylos	*Maianthemum-Viburnum*
Vaccinium scoparium	*Aster-Gaultheria*
Calamagrostis-Arctostaphylos	*Aster-Corylus*
Calamagrostis Vaccinium	*Aster-Aralia*
Calamagrostis	*Aralia-Oryzopsis*
Hylocomium-Ledum	*Hylocomium-Cornus*
Vaccinium-Gaultheria	*Vaccinium-Gaultheria*
Vaccinium-Myrica	*Vaccinium-Myrica*
Vaccin.-Rubus-Papilionaceae	*Maianthemum-Carex*
Pachystima type	*Viburnum*
Calamagrostis-Pachystima	*Oxalis-Cornus*
Pachystima-grass-herb	*Bazzania-Oxalis*
Pachystima Vaccin. parvifol.	*Cornus-Maianthemum*
Pachystima Coptis	*Viburnum-Oxalis*
Oxalis-Hylocomium	*Oxalis-Hylocomium*
Hylocomium-grass-herb	*Hylocomium*
Tiarella-Vaccinium	*Mitella*
Tiarella Fern	*Aspidium-Oxalis*
Fatsia-Fern	*Dicentra*

Complete sociological analyses of these communities would lead to a better understanding of their biotic relationship, and their present and prospective utilization.

Pine forests of the southern parts of the United States (Long Island southward) are conspicuously open between the low shrub layer, or even the ground layer, and the crowns of the trees. The dominant tree may be *Pinus rigida, P. Taeda, P. echinata, P. palustris* or *P. caribbaea.* Many descriptions of these forests, more or less exact in nature, have been published (Harper, Shreve, Stone), but nothing so comprehensive as that by Billings (1938) on stands of *Pinus echinata* in North Carolina.

Billings examined stands of known age from 9 to 110 years. The entire phanerogamic flora of the stands was considered, and critical records of soil conditions were made. We have thus a picture of the march of vegetation after abandonment of agricultural land, along with the development of a new woodland soil. Abandoned land in this region "is first occupied by a relatively shallow-rooted herbaceous community dominated by broom-sedge (Andropogon virginicus)." Pine invades this, followed by oaks and hickories. Meanwhile a ground vegetation characteristic of broadleaf stands develops as the pines grow older. Pine reproduction ceases, and deeper-rooted broadleaf trees take the place of pine.

The surface soil shows "a progressive decrease in volume-weight and increase in water-holding capacity" through the pine stages. This is just the reverse of what happens when trees invade the richly humic prairie soils. "The profile seems to be affected by pine only in the first six inches of soil. An A_1

horizon has developed in this region. This horizon becomes lighter and more retentive of water throughout the pine succession because of the addition of organic matter, the formation of root channels, and the activities of the soil fauna. These causal factors in soil change are conditioned by the presence of pine vegetation which in turn is changed and eventually disappears because of its effect on its own environment."

The tropical forest is often referred to as the most complex biocoenose in existence. And doubtless it is. But there are many types of tropical forest. The tropical rain-forest is described by geographers as so dark and somber that but little vegetation exists below the crowns of the trees. The jungle is on the drier margins of this forest, where the tree-canopy is less dense and enough light filters through to give life to an amazing abundance and density of undergrowth. The tiger who prowls in these thickets must be flattened laterally, like the flea who prowls among the hairs of a dog. At places in the Blue Mountains of Jamaica the entire height of the forest is so dense with vegetation, terrestrial, epiphytic and parasitic, that one can hardly speak of layering (Johnson, D. S., F. Shreve et al. in litt.).

The immense number of species and genera of trees in the tropical forest is an obstacle to any kind of sampling by quadrats (Gleason & Cook 1927). The height of the canopy makes recognition of species difficult. The minimal area for sampling reaches super-human dimensions.

On the other hand, the bamboo forests of India described by Stapf consist of but one dominant species. They are really super-man-size cane brakes, with a seasonal growth of 40 years instead of 8 or 10 months, but with just as sharp a periodicity. For at the end of their years of immaturity the whole countryside bursts into bloom, an immense crop of gigantic grass-seeds is matured and dropped to the ground, and the miles and miles of dead bamboos whiten in the sun and fall and lodge in an impenetrable mass.

The difficulties of the plant sociologist in the tropics have been partly overcome. We have a number of associational studies already, with more to follow. Davis & Richards (1933-34) should be consulted.

Communities of Lower Rank

It remains to discuss briefly some communities that are not admissible to the rank of Association in the international sense.

Lichen communities are familiar to every field botanist. They are saxicolous, terricolous, corticolous and, in the tropics, foliicolous. Saxicolous communities are affected by chemical composition of the rock, hardness, sun and shade, nitrogen content of the water supply, as well as climatic and historical factors. Fink (1904, 1917) and Cooper (1928) have discussed the settlement of lichens on rocks and their rate of growth. Corticolous communities are affected by water-holding capacity of bark, hardness of bark, permanence, shade, "microclimate." Cain & Sharp (1938) have shown that corticolous moss communities ("unions") differ according to the tree community, the species of tree and the height above the ground. Billings & Drew (1938) have measured some of the habitat factors of the unions studied by Cain & Sharp. Ochsner and others have made similar studies.

Saxicolous communities of mosses are influenced by the same factors as are lichen communities. Of the countless miscellaneous glacial boulders around the shores of Lake Okoboji, Iowa, only certain non-calcareous rocks are inhabited by *Ulota americana*.

The one-layered communities or unions of vascular plants studied by Lippmaa and others are distinct entities. Cajander, Ilvessalo, Heimburger and others find these communities under various forest canopies. It is for this reason that these scholars consider one-layer communities more significant than the trees themselves as indicators of the quality of forest sites. To the Zürich-Montpellier sociologist, however, they are layers of the forest association.

Concluding Remarks

It would be impossible in this paper to list all of the plant associations on land that have been described. Conard (1935) listed 71 for central Long Island. Tüxen (1937) gives 41 alliances, each with 1 or more associations for the Province of Hannover. The Montpellier Prodromus is in its 5th Fascicle. From the mass of available material we have tried to select representative examples, with a view to pointing out the different kinds of problems that have been encountered.

The understanding of plant communities is a worthy aim in itself. And in addition such an understanding is essential in enabling us to make the best use of land. No method of examination and description of vegetation has been so productive and suggestive as that of the recent plant sociologists. For the juxtaposition of plants in communities is not only an empirical generalization. The association of individuals and species is much more than a chance meeting. It is a part of the order of nature. And upon the plant community depends the animal community, including communities of our own species.

Summary

1. The procedures and concepts followed by plant ecologists have been greatly influenced by the nature of the communities studied.

2. Distinguished scholars and teachers have largely dominated the thought of pupils and followers in their respective countries.

3. The study of the composition of communities has led to definitions of Associations and Unions, with subdivisions and super-categories.

4. Associations of plants on land are definable entities, susceptible of naming and classifying.

5. Associations extend from simple one-layered communities of lower plants (algae, lichens) to the extremely complex tropical jungles.

6. Unions (one-layered communities) offer fruitful materials for study, within the Association.

7. The goals of Plant Sociology are

1. An understanding of the Order of Nature,
2. Directions for the wisest use of land.

REFERENCES

ALBERTSON, F. W. 1937—Ecology of mixed prairie in west central Kansas. Ecol. Mongr. **7**:481-547.

ALWAY, F. J., J. KITTREDGE AND W. J. METHLEY. 1933—Composition of the forest floor layers under different forest types on the same soil type. Soil Sci. **36**:387-398.

BHARUCHA, F. R. 1932—Etude écologique et phytosociologique de l'Association à Brachypodium ramosum et Phlomis lychnitis des Garigues Languedociennes. Stat. Internat. Géobot. Médit. et Alp. Comm. **18**. Montpellier.

BILLINGS, W. D. 1938—The structure and development of old field shortleaf pine stands and certain associated physical properties of soil. Ecol. Monogr. **8**:437-499.

——— AND W. B. DREW. 1938—Bark Factors affecting the distribution of corticolous Bryophyte Communities. Amer. Midl. Nat. **20**(2):302-330.

BLIZZARD, A. W. 1931—Plant Sociology and Vegetational Change on High Hill, Long Island, N. Y. Ecology **12**:208-231.

BRAUN-BLANQUET, J. 1913—Die Vegetations-verhältnisse der Schneestufe in den Rätisch-Lepontischen Alpen. Neue Denks. d. Schweiz. Naturforsch. Ges. **48**: 1-347.

———1932—Plant Sociology. Transl., etc., by Geo. D. Fuller and H. S. Conard. McGraw-Hill, New York.

———1933—Prodrome des Groupements Végétaux. Fasc. **1**. Montpellier.

———1935-36—Bibliographia Phytosociologica. Fasc. **1**, Allemagne. **2**, Pays-Bas. **3**, Regio Mediterranea. Montpellier.

———1936—La Chenaie d'Yeuse méditerranéenne (Quercion ilicis). Sta. Intern. Géobot. Med. et Alp. Comm. **45**. 147 pp. Montpellier.

———1936a—Prodrome, Fasc. **3**.

——— AND M. MOOR. 1938—Prod. Pflanzengesellschaften. Fasz. **5**.

CAIN, S. A., M. NELSON AND W. MCLEAN. 1937—Andropoganetum Hempsteadi: a Long Island grassland vegetation type. Amer. Midl. Nat. **18**:334-350.

——— AND A. J. SHARP. 1938—Bryophytic unions of certain forest types of the Great Smoky Mountains. Amer. Midl. Nat. **20**(2):249-301.

CAJANDER, A. K. 1909—Über Waldtypen. Acta Forest. Fenn. **1**.

———1926—The theory of forest types. Acta Forest. Fenn. **29**:1-108.

——— AND Y. ILVESSALO. 1921—Über Waldtypen II. Acta Forest. Fenn. **20**.

CANNON, W. A. 1911—Root habits of desert plants. Carnegie Inst. Wash. Publ. **131**.

CLEMENTS, F. E. 1905—Research methods in Ecology. Lincoln, Neb.

———1916—Plant Succession. Carnegie Inst. Wash. Publ. **242**.

———1920—Plant indicators. Carnegie Inst. Wash. Publ. **290**.

———1934—The relict method in Dynamic Ecology. Jour. Ecol. **22**:39-68.

——— AND E. S. CLEMENTS. 1933—Carnegie Inst. Wash. Year Book **32**:203-4.

CONARD, H. S. 1935—The Plant Associations of Central Long Island. Amer. Midl. Nat. **16**:433-516.

———1938—The fir forests of Iowa. Proc. Iowa Acad. Sci. (1939).

COOPER, W. S. 1928—Seventeen years of successional change upon Isle Royale, Lake Superior. Ecology **9**:1-5.

COVILLE, F. V. AND D. T. MACDOUGAL. 1903—Desert Botanical Laboratory of the Carnegie Institution. Carnegie Inst. Wash. Publ. **6**.

COWLES, H. C. 1899—The ecological relations of the vegetation of the sand dunes of Lake Michigan. Bot. Gaz. **27**:95-117, 167-202, 281-308, 361-391.

———1901—The physiographic ecology of Chicago. Bot. Gaz. **31**:73-108.

DAVIS, T. A. W. AND P. W. RICHARDS. 1934—The vegetation of Moraballi Creek, British Guiana: an ecological study of a limited area of tropical rain forest. Part II. Jour. Ecol. **22**:106-155.

DIELS L. 1929—Pflanzengeographie. Berlin.

FAEGRI, K. 1937—Some recent publications on Phytogeography in Scandinavia. Bot. Rev. **3**:425-456.

FINK, B. 1895—The Lichens of Iowa. Bull. Lab. Nat. Hist., State Univ. of Iowa, **3**(3).

———1904—A lichen society of a sandstone riprap. Bot. Gaz. **38**:265-284.

———1917—The rate of growth and ecesis in lichens. Mycology **9**:138-158.

FRIEDEL, H. 1938—Boden-und Vegetations-entwicklung im Vorfelde des Rhonegletschers. Vorl. Ber. Geobot. Forschungsinst. Rübel f. **1937**:65-76.

GLEASON, H. A. AND MEL T. COOK. 1927—Plant Ecology of Porto Rico. Sci. Surv. Porto Rico and the Virgin Islands **7**, parts 1 and 2 N. Y. Acad. Sci.

GRIGGS, R. F. 1933—The colonization of the Katmai ash, a new and inorganic soil. Am. Jour. Bot. **20**:92-113.

———1936—Hepaticae as pioneers on nitrogen-free volcanic ash. Ann. Bryolog. **8**:74-79.

HANSON, H. C. 1938—Ecology of the Grassland. Bot. Rev. **4**:51-82.

———AND W. WHITMAN. 1938—Characteristics of major grassland types in western North Dakota. Ecol. Monogr. **8**:57-114.

HARPER, R. M. 1908—The Pine Barrens of Babylon and Islip, Long Island. Torreya **8**:1-9, figs. 1-2.

———1917—A quantitative, volumetric and dynamic study of the vegetation of the Pinus Taeda belt of Virginia and the Carolinas. Bull. Torrey Bot. Club **44**(1):39-57, fig. 1.

———1917—The Natural Vegetation of Western Long Island, South of the Terminal Moraine. Torreya **17**:1-13.

———1922—Cape Cod Vegetation. Torreya **21**:91-98. No. 6 (1921).

HEIMBURGER, C. 1933—The soil question in Canadian forestry. Forest. Chron. **9**:66-73. Ref. in Biol. Abstr. **9**:1358, No. 12229.

———1934—Forest-type studies in the Adirondack region. Cornell Univ. Agric. Exp. Sta. Mem. **165**.

HENSLOW, G. 1894—The origin of plant structures by self-adaptation to the environment, exemplified by desert or xerophilons plants. Jour. Linn. Soc. Lond. Bot. **30**:218.

ILVESSALO, Y. 1922—Vegetationstatistische Untersuchungen über die Waldtypen. Acta Forest. Fenn. **20**.

———1929—Notes on some forest (site) types in North America. Acta Forest. Fenn. **34**:1-111.

JONES, G. N. 1936—A botanical survey of the Olympic Peninsula, Washington. Univ. of Wash. Publ. Biology **5**.

KERNER, A. 1863—Das Pflanzenleben der Donauländer. Edited by F. Vierhapper. Vienna, 1929.

LIPPMAA, T. 1935—Une analyse des Forêts de l'Isle Estonienne d'Abruka (Abro) sur la base des associations unistrates. Acta Inst. et Hort. Bot. Univ. Tartu. **4**(1-2).

LOEHWING, W. F. 1937—Root interactions of plants. Bot. Rev. **3**:195-239.

MCDONALD, SISTER E. S. 1937—The Life-Forms of the Flowering Plants of Indiana. Amer. Midl. Nat. **18**:687-773.

MAIRE, R. 1924—Études sur la végétation et la flore du Grand Atlas et du Moyen Atlas marocains. Mém. Soc. Sci. Nat. Maroc. **7**.

———1925—Carte phytogéographique de l'Algèrie et de la Tunisie Algèr.

———1928—La végétation et la flore du Hoggar. Bull. Soc. Hist. Nat. de l'Afrique du Nord.

MOOR, M. 1936—Zur Soziologie der Isoetetalia. Beitr. z. geobot. Laandesaufn. d. Schweiz **20**. Bern.

———1937—Prodromus der Pflanzengesellschaften. Fasz. **4**. Leiden.

MOTYKA J. 1926—Studien über epilithische Flechtengesellschaften. Bull. Acad. Pol. Sci. Lettres B.

NORDHAGEN, R. 1928—Die Vegetation und Flora des Sylenegebietes. I. Die Vegetation. Oslo.

OCHSNER, F. 1928—Studien über die Epiphytenvegetation der Schweiz. Jahrb. St. Gall. Naturw. Ges.

OLMSTED C. E. 1937—Vegetation of certain sand plains of Connecticut. Bot. Gaz. **99**:209-300.

OOSTING, H. J. AND L. E. ANDERSON. 1937—The vegetation of a barefaced cliff in western North Carolina. Ecology **18**:280-292.

PAVLYCHENKO, T. K. 1937a—The Soil-block washing method in quantitative root study. Canad. Jour. Research, Sec. C, **15**:33-57.

———1937b—Quantitative study of the entire root system of weed and crop plants under field conditions. Ecology **18**:62-79.

RAUNKIAER, C. 1934—The life forms of plants and statistical plant geography. Oxford.

REYNAUD-BEAUVERIE, M. A. 1936—Le Milieu et la Vie en commun des Plantes. Lechevalier, Paris.

RÜBEL, E. 1930—Pflanzengesellschaften der Erde. Hans Huber, Bern-Berlin.

———1932—Die Buchenwälder Europas. Veröff. d. Geobot. Inst. Rübel in Zürich **8**. Bern.

———1936—Plant communities of the world. Essays in Geobot. in honor of W. A. Setchell. University of Calif.

SCHROETER, C. 1926—Das Pflanzenleben der Alpen. Zürich. 1288 pp.

SHREVE, F. 1936—Plant Life of the Sonoran Desert. Sci. Monthly **42**:195-213.

——— AND A. L. HINCKLEY. 1937—Thirty years of change in desert vegetation. Ecology **18**:463-478.

———ET AL. 1910—The Plant Life of Maryland. Johns Hopkins Press.

SIPLE, P. A. 1938—The second Byrd Antarctic Expedition—Botany. I. Ecology and Geographical Distribution. Ann. Mo. Bot. Gard. **25**:467-514.

STONE, W. 1911—The plants of southern New Jersey with special reference to the flora of the Pine Barrens and the geographic distributions of the species. Ann. Rep. New Jersey State Mus. **1910**:23-828.

SVINHUFVUD, V. E. 1937—Untersuchungen über die bodenmikrobiologischen Unterschiede der Cajander'schen Waldtypen. Acta Forest. Fenn. **44**:1-63.

SZAFER, W. 1924—Zur soziologischen Auffassung der Schneetälchenassoziationen. Veröff. d. geobot. Instituts Rübel in Zürich **1**.

THONE, F. 1915—Pioneer Plants of a new Levee. Proc. Iowa Acad. Sci. **22**:135-142; **23**:423-426; **24**:457-458.

THORNBER, J. J. 1909—Vegetation Groups of the Desert Laboratory Domain. Carnegie Inst. Wash. Publ. **113**, Chap. IV.

TÜXEN, R. 1930—Über einige nordwestdeutsche Waldassoziationen von regionaler Verbreitung. Jahrb. Geog. Ges. Hannover.

——— 1937—Die Pflanzengesellschaften Norwestdeutschlands. Mitt. d. Flor. soziol. Arbeitsgemein. i. Niedersachsen. **3**. Hannover.

——— UND W. H. DIEMONT. 1936—Weitere Beiträge zum Klimaxproblem des westeuropäischen Festlandes. Mitth. d. Naturw. Ver. zu Osnabrück **23**:130-184.

WATT, A. S. 1923—The ecology of British beech woods. Jour. Ecol. **11**:1-48.

——— 1925—Development and structure of beech communities. Jour. Ecol. **13**:27-73.

——— 1934—The Vegetation of the Chiltern Hills, with special reference to the beechwoods and their seral relationships. Jour. Ecol. **22**:445-507. Ref. in Biol. Abstr. **11**:1941, no. 18071.

——— 1935—Some Climax Associations of Great Britain. Proc. VI. Internat. Bot. Congr. Amsterdam. **2**:66-68.

——— AND G. K. FRASER. 1933—Tree roots and the field layer. Jour. Ecol. **21**:404-414. Ref. in Biol. Abstr. **10**:14, no. 128.

WEAVER, J. E. 1919—The ecological relations of roots. Carnegie Inst. Wash. Publ. **286**.

——— 1920—Root development in the grassland formation. Carnegie Inst. Wash. Publ. **292**.

——— AND F. E. CLEMENTS. 1929—Plant Ecology. McGraw-Hill, New York. 1938, Ed. 2.

——— AND T. J. FITZPATRICK. 1920—Ecology and relative importance of the dominants of tall grass prairie. Bot. Gaz. **93**:113-150.

——— AND W. J. HIMMEL. 1931—The environment of the prairie. Conserv. Dept. Conserv. and Surv. Div. Univ. Nebraska Bull. **5**:1-50. Ref. in Biol. Abstr. **6**:370, no. 3399.

——— AND T. J. FITZPATRICK. 1934—The Prairie. Ecol. Monogr. **4**:109-295.

GRINNELL COLLEGE,
GRINNELL, IOWA.

DISCUSSION

Park: The layers in certain of these associations are said to be interdependent and I should like to know of what the proof consists.

Conard: The most conspicuous example would be where acidic soil is produced by the presence of coniferous trees, and the ground layer of vegetation becomes typically acidic, as described by Billings (Ecol. Monogr. 8:437-499, 1938). He shows clearly how in revegetation of abandoned agricultural land in the Duke Forest in North Carolina the pines come in and by their action add humus to the sand making it lighter in weight and more retentive of water.

Gleason: Another good example is the density of the lower strata under the forest canopy. The amount of this lower vegetation depends directly on available light, and this is controlled by the forest canopy.

Lippmaa: Phytosociology as a science is relatively young. This situation may also in part be responsible for the differences of interpretation of such terms as "association", "sociation", etc. The vegetation of Switzerland, if compared with the vegetation of Scandinavia, is really not so different in view of the many similarities, especially with the mountains of Norway and Sweden. The ecological viewpoint has been much more developed in Central Europe by Kerner, Schröter, and others, than in Scandinavia with its highly developed taxonomic and statistical studies.

Is the soil really the product of vegetation? Is it independent of the parent rock? In the Sahara we found an area of perhaps ten square kilometers with very different soil conditions: sand, loam and rock. The vegetation of sand with *Retama retam, Genista Saharae*, etc. is entirely different from the vegetation on the loamy ground *(Fredolia aretioides)* and from the vegetation of rocks (*Warionia Saharae*, etc.). In central and northern Europe are found, for example, sandy, loamy and peaty soils. Neither vegetation nor climate even when it is a podsol climate can change peat soil into sand or loam, or sand into loam.

Carpenter: If it were given a sufficient length of time probably the soil would actually change. The spread of forbs in the prairie makes it almost impossible to define association in the international sense. What unit does the prairie as a whole represent?

Conard: I have no unit for it. This hasn't been studied.

Steiger: Many of Braun-Blanquet's methods and sociological concepts are misinterpreted and much analytical work must be done here before a system of units can be worked out.

Cain: Perhaps investigators who have traveled as widely as Clements and Rübel, may not, as a consequence of their experience, have much faith in fidelity. This does not mean that fidelity is not an accurate concept for some communities, which can be classified on that basis. It simply means that fidelity is a local phenomenon, since a certain species may be a calciphile in one place and a calciphobe in another. The variation may be taken as an indicator of the changes in fidelity. Thus Braun-Blanquet's scheme, so adequate in local regions, proves inadequate if applied to a larger area.

Steiger: But an association should not be recognized over too large an area.

Cain: That suggests, of course, the perennial question: How many species must remain to preserve the identity of the association? It is doubtful that a satisfactory answer will ever be found.

Littoral Marine Communities

G. E. MacGinitie

Discussion of Terminology

The use of terms relating to ecology, particularly animal ecology, impresses me as being somewhat in a state of confusion. I suppose that in a conference of ecologists one could get as many definitions of the term "community" as there are ecologists present. The same would be almost as true of the term "ecology" itself. Elton's definition (1927) (which is one of the shortest): "Ecology is scientific natural history," though good, I think is open to criticism, because natural history statements, if true, are scientific facts, for they are capable of being incorporated in the science of biology, and the subscience of ecology. If they are not facts, then they are not natural history. Shelford's definition (1929), "Ecology is the sociology of organisms," emphasizes too much the interrelationship of organisms and not their environmental adaptations. The definition that one sometimes hears, "Ecology is the study of animals in relation to their environment," gives somewhat the opposite impression — that the environment is the important phase. A combination of the two, that ecology is the study of the social life of animals and their relation to their envoronment, would seem to be much more correct and to the point, yet, to me, it seems that this definition still leaves out a very important part of ecology, as I will attempt to show later in this paper, that of the individual life history. The individual organism is the unit of ecology, and, therefore, a study of the unit is just as much a part of ecology as the study of a particular cell may be to the study of physiology or morphology. If we keep this fact in mind, that a knowledge of the social activities of an animal community is not known until the individual life histories are known, then our definition, "Ecology is the study of the sociology of animals and their relation to their environment," satisfies the objective to be obtained by the study of ecology. King and Russell (1909) give what I consider the best definition I have seen in print: "The study of the relations between animals and their environment, both animate and inanimate." Some consider environment to be inorganic or at least inanimate. Webster says that it is the sum total of all external factors which affect the organism.

The term "animal communities" is often used synonymously with "animal associations." Webster's dictionary defines an ecological association as "an assemblage of plants," so suppose for now we leave "associations" as a term to be used by the plant ecologists, and turn to the definition for community,[1]

1 The term "community" is used rather loosely in this paper as it supplies a general implication of what is meant. It can not be used concisely until a more definite method of delimiting communities is devised. The same is true for the terms "dominant" and "dominance." There are all degrees of dominance, therefore the dominant animal can not be used in all cases to name a community.

which, to quote, is: "An assemblage of animals or plants living in a common *home,* under similar conditions of environment, *or* with some apparent association of *interests.*" For my part I am quite willing to accept this definition, except that I should like to change the word "home" to "locality," and the second "or" to "and," and the word "interests" to "activities or habits." A marine animal has no more "interest" in anything than has a tree. This paper, then, will deal with assemblages of marine animals, each essemblage living in a common locality, under similar conditions of environment, and with some apparent association of activities or habits.

Some Important References

Work done on the fauna of marine communities from an ecological point of view is somewhat meager. Considerable has been written which pertains to ocean animals, but most of it has been done from a taxonomical, morphological, physiological, and, to a lesser extent, natural history point of view. It has always been the tendency to do the type of work which can be done in a laboratory. Relatively few attempts have been made to treat of marine communities. Much of the work which has been done that can be said to apply to marine animal communities has been pioneering work, and, therefore, a great deal of variation is shown in the method and technique of such work.

The pelagic environment will be omitted from this paper as it is outside the realm of my activities and could be much better discussed by someone else. Because of the interest in oceanographic activities, and its side line of biological investigations, much has been done and written in this field. I believe that a comprehensive arrangement of the material already available would supply a very good cross section of pelagic communities, at least in the North Atlantic.

Since Gislen's history of marine sociology (see below) is so complete, I shall not review what he has already done better than I could do. But I should like to mention some general works on marine sociology and later make reference to other papers as they come to have pertinent application to the different habitats.

I regard Hesse's Ecological Animal Geography, as revised by Allee and Schmidt (1937), as the best reference book that we have in animal ecology today. It has done that thing which I think so important at the present time: it has comprehensively arranged the general principles relating to animal ecology. Here at last we have a general reference book for ecology which leaves little to be desired. However, with the exception of coral reefs, it has practically ignored the Pacific Ocean as far as marine animals are concerned, and some of the generalizations made do not hold true for this region. Its bibliography and that of Shelford's Laboratory and Field Ecology (1929) are so extensive that no bibliography will be included in this paper except to give references pertinent to statements made herein, and certain references to Pacific Coast animals which were omitted from the two works just cited.

The response which one usually gets when asking others what they think of Shelford's Laboratory and Field Ecology is, to quote: "It contains a fine bibliography." The title, Laboratory and Field Ecology, correctly depicts the contents. It deals mostly with laboratory procedure, is highly technical, and makes use of terms which are ill-defined, and is of little help in the real ecological laboratory, namely, the field. My impression, an impression which has been derived entirely from Dr. Shelford's writings, is that he is, for some reason, averse to making use of individual life histories, in other words he tends to ignore the fundamental unit of ecology, that of the living organism. However, he makes what seems to me a much graver mistake by attempting to use unit factors as criteria for occurrence, abundance, distribution, etc. in animal communities. I firmly believe that it is impossible for one to get the "feel" of animals in their ecological relationships without having done considerable natural history work. It seems to me that I can sense a decided change at the present time in Dr. Shelford's writings from what they have been in the past. I think he is becoming more liberal in his attitude toward life history work, and I have noted that certain of his students decidedly sense their lack of knowledge of natural history and the handicap that it has placed upon them (for example, see Rice, 1930). When one disregards the fundamental unit of a science the aspect is like looking into the large end of a horn. As a result of such disregard, one's writings and concepts tend to show vagueness and there is also a tendency for them to lack vitality and interest, which is not so true of the writings of those who have more background in natural history.

The Epibioses of the Gullmar Fjord, by Gislen (1929, 1930), is an excellent piece of work on marine animal communities, yet its usefulness is limited by its lack of such information as growth studies, life histories, etc. In the forepart of Part II Gislen (1930) gives a complete history of the sociological work on the marine animal communities up to and including 1929. The completeness of this review is shown by his own statement: "I am certainly aware of the fact that possibly there may be some solitary marine sociological work which has escaped my attention, but I wish to emphasize that the exhaustive history . . . is relatively, if not absolutely, in any case the most complete which has yet been presented." Knowing Dr. Gislen and the thoroughness of his work as I do, this is not a boast, but a mere statement of fact. For a history and bibliography of marine ecology up to 1930 one needs no other reference than Gislen, Shelford, and Hesse. Shelford's bibliography is much more conveniently arranged than that of Hesse's.

Petersen's investigations of the Danish sea-bottom, though prior to 1930 (1913, 1918) is a very good piece of work on marine communities. It, however, like all sea bottom investigations, is handicapped because sufficient sampling of the substratum was not done, and, therefore, judging from the experience I have had with bottom communities, data on at least a third of the community is lacking.

Practically no extensive studies have been made of sandy beaches. Considering the extent of sandy shores throughout the world, this statement may

come as something of a shock, and indicates how little has been done on marine animal communities.

Certain Environmental Factors of a Sand Beach in the St. Andrews Region, New Brunswick, with a Preliminary Designation of the Intertidal Communities, by C. L. Newcombe (1935), is an interesting paper on what he calls two sand beach communities. The information it contains relative to the rate of evaporation from different grades of beach sand is not only a very worth while part of his paper, but of great value to all those concerned with marine animal communities in sandy regions. I have often been impressed with the way in which the sand and mud maintain a low temperature, due to the factor of evaporation. As long as the sand is wet and evaporation is going on, there is little rise in temperature in the exposed sand or mud. When, however, a layer on top becomes sufficiently dry to cut down the evaporation, the temperature of this layer rises very rapidly. But, fortunately, because of the relatively short time that the sand or mud is uncovered, these high temperatures penetrate, as Dr. Newcombe has said, to only a very few inches, in our regions seldom more than two or three inches. If I were to offer any criticism of Dr. Newcombe's paper it would be that the title should have included rocky beach, for any rock which is sufficiently stable to maintain a crop of *Balanus* is true rocky beach. Another interesting fact about the paper just cited is that shown by so many ecological papers, and which is indicative of the lack of uniformity of concepts relating to animal communities: it gives many definitions, as do most ecological papers (this one included), which definitely shows that one of the first needs for the ecological worker is more standardization of terms, and, I think, simplification of terms.

Hewatt's Ecological Studies on Selected Marine Intertidal Communities of Monterey Bay, California (1937), is a fine contribution to rocky shore communities, but has its limitations because it lacks growth studies, life histories, etc. It also needs comparison with other rocky shore communities.

My own Ecological Aspects of a California Marine Estuary (1935) I hope has contributed to the knowledge of smooth bottom communities. It has many deficiencies. It would take many more years of work to anywhere nearly complete the fundamental knowledge which should be a part of such a work. Other criticisms will be evident as I later discuss particular habitats.

Many other investigators are constantly contributing studies which will be of great value to supplement more detailed generalized studies of marine communities, for example, Weymouth's Life History and Growth of the Pismo Clam (1923), and Coe and Allen's Growth of Sedentary Marine Organisms on Experimental Blocks and Plates for Nine Successive Years at the Pier of the Scripps Institution of Oceanography (1937).

The Relation of Marine Animal Communities to Ecology

For certain Reasons, the study of marine communities has many unique aspects when compared with terrestrial communities. Some of the factors which make marine communities different from those of land communities are: less

variation in temperature, a slower metabolic rate in the animals, a more ample and easily obtained food supply, in general, more lavish reproduction among the animals, no social activities, and a lack of intelligence on the part of the animals. Because of this lack of intelligence, all activities are purely instinctive, and, for this reason a study of marine communities causes one to realize that instinct is just as much a part of the inheritance of an animal as are morphological or physiological characters, and, if one wishes to make comparisons, even more important. If one excludes the flying insects and those which prey upon them, such as birds and bats, there is no plankton and there are no plankton feeders on the land. In the sea, then, despite its fringe of seaweed and because of the unseen nature of its meadows, it is quite evident that animals, both sessile and moving, are the obvious organisms to be dealt with. Attention centers naturally upon the fauna, and, therefore, I trust that I am not wrong when I say that it is from the *marine* animal communities that we should be able to get many of our fundamental concepts of animal communities.

I do not believe that the seaweeds should be afforded a very important place in marine animal communities, because the influence which they exert on a marine animal community is somewhat similar to that of the rocks to which they are fastened, that is, they form a refuge. They are used to little extent by the animals as food, and, though I am well aware that their distribution often coincides with that of some of the so-called dominant or predominant animals of the rocky region, on the whole they exert little influence other than that of protection.

Variation in Marine Animal Communities

We often speak of the static condition of marine environments as compared with those of the land, but, strictly, this is not true. Relatively speaking, the marine environment is subject to much less variation than are land environments, but after all, there is nothing static about marine communities, and the adaptations of marine animals to the extremes of their environment are proportional to these extremes, that is,

$$\frac{\text{marine animals}}{\text{marine environment}} = \frac{\text{terrestrial animals}}{\text{terrestrial environment}}.$$

As the years go by I have been more and more impressed by this factor of variation in marine habitats. There seems to be a tendency for those who write papers about marine animals, or, for that matter, animal communities in general, to give the impression that the picture presented of the animal community is one which will be the same at any time in the future, and that practically all of the necessary or important work on the animal community has been completed. Nothing could be further from the truth, and I, for one, am very glad, for it is the change, in other words, the variation shown by these animal communities and the individuals that comprise them which make them so interesting. For example, because of the opportunity for comparison, a second study of the area Hewatt describes in his paper (1937), or a second

thorough study of Elkhorn Slough, would give us more information of a valuable nature than did the first papers in either case.

To show how important is this factor of variation not only in a short time but in limited space, I would like to present a brief discussion of three *Mytilus* communities from Monterey Bay, one done by Hewatt (1935), and two done by myself. The latter have never been prepared for publicaion. The following table gives a brief comparison of these three communities, especially as regards the six most common animals.

Comparison of Three Mytilus Communities from Monterey Bay, California

Date Investigator Type of Habitat	Aug., 1930 MacGinitie Rocky Shore	Nov., 1931 Hewatt Rocky Shore	Feb., 1932 MacGinitie Boat Bottom
Six most abundant animals		Number	
Mytilus californianus	613	120.5	376.7*
Cirolana harfordi	3065	69.0	0
Petrolisthes cinctipes	180	30.9	0
Physocosoma agassizi	168	24.4	0
Thais emarginata	60	16.3	0
Amphipods	263	63.2	641.6
Total number of species	22	20	45
Total of all animals	4711	454.2	1637.3
Average weight of Mytilus	34.6		28.3
Average length of Mytilus	38.6		32 6

* See below.

The first community was in a mussel bed on the exposed rocks at Pt. Pinos at Monterey Bay. A quarter square meter of the mussel bed was carefully taken from the rock, the species of animals determined, the numbers of each species tabulated, and the weight of a few of the abundant animals was recorded. The data for the second community was taken from Hewatt's paper (1935), and the third community was represented by four square feet from the bottom of a lighter anchored in Monterey Harbor. As the areas were different in size in each case, they have been reduced to a common denominator in the above table.

Several interesting facts are brought out by the above comparative table. In Hewatt's report he makes the statement: "The population apparently represented a climactic biotic condition, a typical *Mytilus californianus* association." From the photograph on page 245 of his paper it is quite evident that the area he shows was not a typical *Mytilus californianus* association or community. The area selected was too high for this to be true. The upper part could be called a *Balanus glandula-Acmaea* community. Here, again, we are confronted with the necessity for uniformity in our concepts regarding marine animal communities. Comparison between the area I investigated and the area represented in Hewatt's paper shows too much discrepancy for one or the other not to be wrong, since they were both taken from the same mussel bed. The one which I have shown was taken directly from the center of the *Mytilus* colony, and, therefore, represents the maximum to be found in a

mussel bed. Of course, Hewatt's paper was not intended to be representative of a *Mytilus* association, but to show succession, and from this point of view the area he chose was better than if he had taken it lower down. However, I must disagree with the idea that the area he chose was a typical *Mytilus* association or community. It may be said of my sampling of the mussel bed that I should have taken a larger area, but I believe that a careful consideration of the problem will lead to a different conclusion. If only one sample of a community is taken, and that from what could be considered a mid-region, then one gets a picture of the community at its best, and, as no species of marine animal is known to draw a sharp boundary line in its dispersal, surely it is evident that such a sample would be the maximum and would die out toward its boundary limits. The characteristics of the boundary can be made a part of the general discussion of the paper. However, it is certainly obvious to any investigator that it would be impossible to take any two equal areas in a mussel bed and obtain exactly the same results.

As a further contrast I have shown the population of an area from the bottom of a fish lighter which had been at anchor for 2 years and 10 months a distance of about a half mile from the Mytilus communities described by Hewatt and myself in parts one and two of the above table. Because of the large number of juveniles and because it is almost impossible to separate the two species at this age, the number of mussels listed in the community from the bottom of this barge includes the total of both *Mytilus californianus* and *Mytulis edulis,* which occurred in about equal numbers.

It will be noted that, in spite of the fact that *Mytilus* is the dominant or predominant animal in all three communities listed, the communities represented by columns one and two are decidedly different, and, except for *Mytilus californianus,* the third is entirely unlike the other two. It will also be noted that while certain animals profit greatly by the presence of *Mytilus* in the shore community, they are, however, "unwilling" or unable to change their habitat to the extent of following *Mytilus* to the bottom of a barge. While the *Mytilus* from the boat bottom had an average length of 32.6 mm, and a weight of 28.3 gm., those of the shore community had an average length of 38.6 mm. and an average weight of 34.6 gm., showing that the boat bottom community had not yet reached what is sometimes called a climactic condition. Still there was ample time for at least the *Cirolana* and the *Petrolisthes* to have established themselves, and, too, there could by this time have been juvenile *Physcosoma* and *Thais.* Other animals had, however, taken advantage of the protection afforded by *Mytilus* on the boat bottom to occur in considerable numbers, for example, the nestling clam *Saxicava arctica* (264 individuals); the annelid *Halosydna insignis* (95 individuals); the barnacles *Balanus tintinnabulum californicum* (38 individuals) and *Balanus nubilis* (36 individuals); and the annelid *Nereis* sp. (17 individuals).

Although I spoke of variation in size of the *Mytilus,* size is, after all, not a particularly important point. After a mussel bed becomes established, the protection that the mussels afford from the surf, and the refuge that they offer underneath, are the two most important factors in allowing the associated

animals to become numerous. The size of the mussels in the mussel beds along the coast depends to some extent upon their age and the length of time the regular cyclic succession has been under way. On Tillamook rock, off the coast of Oregon, where the food and other factors were optimum, mussels have reached an extreme of 350 mm. in length.

I should like to discuss briefly the first community represented in the table, and to divide the discussion into three parts. First, we could say that by adding the list of other species, with their relative abundance, to the six species already given, and by giving the usual physical and chemical factors of the environment, we would have what is called a typical report on a marine animal community. But, aside from the arousal of a certain amount of passive interest, of what particular value is such data if we stop at this point?

In the second place, however, if we compare this community with others we are forcibly struck by the fact that variation is a very important factor in understanding marine animal communities. And it gives us an opportunity to consider further the idea of dominance. Certainly the mussel has many characteristics of a dominant animal. But we see that the factors of numbers, weight, and size may show considerable variation and are not always good criteria for affording an animal a high rating as a dominant. According to Shelford, then, it leaves only one more criterion, that of influence, upon which to base our justification for calling the mussel a dominant animal. This influence is purely a passive thing on the part of the mussel. As has been said before, its influence consists mainly of affording protection and shelter. The method by which the mussel attaches to rocks affords open spaces underneath, which other animals, for example, barnacles, do not afford. Note, however, that barnacles are also classified as dominant animals by Shelford (1930), Towler (1930), Rice (1930), Worley (1930), and others. The barnacle *Balanus glandula* is dominant because it is so specialized that nothing else can grow where it does, or, if so, only sparsely. By their growth, however, mussels smother out their own kind and eventually give rise to conditions which end in their own destruction and that of many of the animals associated with them. These things may be classified as influence, which, in turn, may be used to designate dominance, but the definition becomes rather complicated when we attribute to the animal influence which, after all, on its part is purely mechanical. It is simply a condition or set of conditions which could be afforded, at least to some extent, by mechanical or inorganic means. The mussel engages in no activity which is definitely done with the purpose of regulating the life of other creatures about it. Its influence, therefore, is purely incidental, it just happens that it affords protection and shelter for many animals. But do not miss the point that *Mytilus* was dominant to an entirely different community on the boat bottom. I sometimes wonder, then, why we make so much of this term "dominance." If one were to write a paper and, instead of using the title "A Mytilus californianus Community," were to use the title "Life in a Marine Mussel Bed," I think the latter would at once furnish a better understanding of what should be contained in the paper and would arouse much more interest on the part of people who saw it than would the

first title. The chances are, too, that it would contain more information of value to the allied subsciences of biology. As I shall show later, it is practically impossible to choose a dominant in other marine habitats. Now, however, by our comparison, we have noted the factor of variation, and, consequently, the *Mytilus* community takes on a more interesting and worth while aspect. And do not forget that variation is the basic factor of evolution, a factor which has made possible the wonderful display of deployment and interrelationship among marine animals.

Suppose now, however, that we are still dissatisfied with the information the mussel community has afforded us and want to know more about how these different animals are associated together. This brings us to the third point of our discussion. Since animals need more than just protection and refuge, we are faced with the question: "How are we going to find out why these creatures are associated together?" I shall not take time or space for more than the five associates listed in the table, or for more than one factor, but, in addition to protection and refuge, suppose we consider the factor of food. *Cirolana harfordi* is a scavenger, living on dead or decaying flesh. Why, then, does it occur in such great numbers in a mussel bed? Mussels smother each other out, and this affords a certain amount of food material for *Cirolana*, but an important reason why the mussel bed is such an excellent place for this small isopod to obtain its food is that the mussel bed acts as a trap for food which is destroyed in the plankton along shore by the heavy surf. Of course, seaweed and rocks also furnish such a trap, but *Cirolana* does not occur so abundantly in such places as in a mussel bed, because the latter provides a greater amount of refuge space than does an equal area of rocky region. The mussel bed acts something like a riffle or the carpet in a miner's box. The food settling out of the water falls into the spaces between the mussels where the flow of the water is at a minimum and where *Cirolana* makes the best of its opportunities. *Petrolisthes cinctipes* is a plankton feeder. It may seem somewhat inconsistent to say that *Petrolisthes* can live on plankton under mussels where other mussels, which also live on plankton, are being smothered out. However, *Petrolisthes* is able to move out nearer the surface of the mussel bed when the tide is in, and the breaking surf not too heavy, and thus get its supply of food. Also, there is something in the idea of the relation of surface and volume, and *Petrolisthes* is a small crab. The peanut worm *Physcosoma agassizi*, with it dendritic spread of tentacles, is able to use plankton and some of the smaller particles of dead material such as the isopod *Cirolana* makes use of. The growth rate of *Physcosoma* is relatively slow, and the amount of food it requires is not very great. *Thais emarginata* is a predacious gastropod. It attacks thin-shelled molluscs, and therefore exerts a great deal of influence on the small mussel crop. It cannot, however, occur in very great numbers until the mussels are large enough to afford it protection; therefore, it can not prevent the original set of mussels to any great extent. One reason why we found the nestling clam so abundant on the lighter bottom was that *Thais* was absent.

Thus we see that when we ascertain factors concerned with the life histories of these creatures there is a good and sufficient reason for their being

where they are. Also, we have thus still further added to the interesting and worth while data to be found in a mussel community by studying the individual life history of each member. What I have said is only a small portion of the valuable information which can be obtained by studying the life histories of individual animals. This information is of value in determining some of the principles which govern their dispersal and evolutional adaptations, and which, in turn, govern the life of these marine creatures. And, incidentally, when I began the study of biology it was my impression that biology is the study of life. It also seems to me that we have added greatly to the value and the understanding of the community by not stopping with the usual procedure of listing the physical and chemical factors of an environment and the animals found therein, but, secondly, by comparing such a community with others of a similar nature, and, thirdly, by studying the natural histories of the individual members of such a community.

There is opportunity here to contrast the animal climactic condition with that of plants. Strictly speaking, there is no such thing as a climactic condition in a mussel bed or any other marine animal community as the term is understood in plant ecology. There certainly is a very close approximation to it in the sand beach community, as will be shown later. But, in a mussel bed the cycle of succession is much like a cycle would be in a plant community if, for example, we had a climactic forest community in which areas here and there were more or less regularly burned so that, over a period of time, the entire forest climax would be subject to destruction and renewal. This is, roughly, what happens in general to marine communities. When the burned forest or the decimated area in the marine community is renewed it is different from what it ever has been before or ever will be again, yet it follows a definite plan because of the adaptation of certain plants or animals to particular regions, and their renewal will conform to the exercise of these adaptive qualities. Therefore we can anticipate the general character of the renewed area if we know these adaptive qualities, and we will know them if we know the natural history of the individual animals which will be the units of the renewed area.

Community Problems of the Mud Bottom

In dealing with the mud flat communities I have found, as has already been brought out (MacGinitie, 1935) that the change may be even greater in two areas which are environmentally identical than was found to be the case in the three *Mytilus* communities just discussed. This is rather interesting because it is generally conceded by zoologists that the mud bottom is the region from which all marine life deployed, hence one might suppose that conditions would be more uniform on the mud bottom than in the regions to which animals have deployed from such a habitat. However, I am inclined to think that from the geological point of view the mud bottom was about the only habitat that marine animals once had. But be that as it may, both the estuarine and ocean floor show very decided differences in different localities which to all outward appearances are practically the same as far as environ-

mental factors are concerned. There is a decided tendency for many marine animals to segregate, and, although the environments may be practically the same, the community may be entirely different. For example, a *Callianassa* (shrimp), a *Urechis* (echiuroid worm), or a *Schizothaerus* (clam) community may occupy a very similar habitat.

In my work on mud flats, though I have found that there is a tendency for animals to form communities, which were somewhat dependent upon such factors as texture of the substratum, tidal exposure, temperature, etc., which is just another way of saying that every animal has its adaptive qualities to a certain set of conditions, I also found that communities were present which were quite different under almost identical conditions. Under such a condition as is exemplified by Newport Bay, Elkhorn Slough, Morro Bay, Humboldt Bay, etc., unless one uses particular regions where a certain animal is dominant and delimits the area by the border of distribution of this animal, it is almost impossible to delimit the region into separate communities, but, instead, it becomes necessary to treat it as a whole or as a single community. If we consider the distribution of a particular animal, for example, any one of those I have mentioned above, we will find that there are patches of them rather widely scattered over the slough bottom. The gaper clam, *Schizothaerus nuttallii*, was found in practically all parts of Elkhorn Slough, but there were three main groupings or colonies, aggregations or communities, whatever they should be called, one being in rather heavy clayey soil, another in sand which was so loose that it would not stand, and another in the eel grass *(Zostera)* region. In each of these three regions, though the gaper clam showed modifications of growth, being rather small and rounded in the heavy mud region, large and symmetrical (up to nearly three pounds in weight) in the loose sand, and of an intermediate size and shape in the *Zostera* region, it was undoubtedly the dominant animal if we accept the term dominant as it is usually used.

Another animal, which shows even more dominant characteristics than the gaper clam, and which is widely distributed in small patches over the slough, is *Phoronopsis harmeri* (?). Where it occurs it grows so closely together that it practically excludes all other forms of life. In contrast with the gaper clam and the phoronid just mentioned, we have such animals as the bent-nosed clam, *Macoma nasuta*, which is distributed throughout all of the region being discussed. With the exception of the *Phoronopsis* communities, this clam invades all the other communities mentioned above. Though it can not be classified as a dominant, still, by the criteria used to determine dominance, it makes a fairly good showing in this respect. If we compare *Phoronopsis* and the bent-nosed clam we have two extremes, either one of which may possibly be considered as an animal best suited to name a community. The one community, which would include the entire area of the portion of the slough studied, could be delimited by the distribution of the bent-nosed clam, *Macoma nasuta*. However, if we use *Phoronopsis* as a dominant animal, and certainly no other animal in the slough region meets the requirements of a dominant animal so well as it does, then we would have several *Phoronopsis*

communities ranging in extent from perhaps a hundred square feet to an acre. And, while *Phoronopsis* was somewhat narrowly limited by the texture of the substratum, it still occupied regions which were practically identical with those of the other animals listed above. Each of these in turn would then occupy many separate habitats and, therefore, represent many separate communities. Then one would be faced with the problem of having such a region as Elkhorn Slough divided into a great many communities, some of which would be very small, and of having practically identical communities which are found under different environmental conditions. Why should one have identical communities under different environmental conditions? The distribution of any animal species may be outlined by the curve of normal distribution. It will have a maximum and a minimum relation to an optimum condition. Hence, one will find a patch of *Phoronopsis* at one end of the curve of normal distribution in sandy mud, and at the other end another patch in muddy sand. For the most part, its associates, what few there are, are more widely distributed than is *Phoronopsis*, and, therefore, the colonies will be practically identical under different environmental conditions. And, too, we will find communities of the other animals interspersed with the *Phoronopsis* communities. If we compare this situation with that of a plant association, we will find that the plant association has its dominant extending over a wide area, but in the mud flats of such regions as Newport Bay, Elkhorn Slough or Tomales Bay there is no such organism. It is a patch work quilt, a Joseph's coat.

It seems to me that there are two solutions to the problems of delimiting communities under such conditions. One is to treat the region as a whole, and when all is said and done, such regions as Newport Bay, Elkhorn Slough, or similar estuaries are not sufficiently different in any part that they could not be considered a single environment, and therefore, the term best suited to such a community would be an estuarine community. It would have no dominant, however, and, therefore, could not be named for animal genera or species. On the other hand such areas may be divided into a great many communities, which would show definite boundaries, but which would be very confusing from an environmental point of view.

What can be said about the surface animals of such regions as I have discussed? Here the situation is even more complicated than is that of the substratum. There are surface communities that remain fairly fixed, as far as environmental conditions or particular localities are concerned. Among these are such animals as the crab *Pugettia producta*, which remains hidden among the *Zostera* in the day time and from where it forages at night for its food. The same can be said of the crab *Hemigrapsus nudus*. These two crabs occur in about equal numbers in the *Zostera*, and their habits are closely similar, except that *Pugettia* is more of a vegetarian, while *Hemigrapsus* is omnivorous. Which one is dominant? In contrast with these we have such colonies or communities as the gastropods *Haminoea vesicula* and the sea hare, *Tethys californica*. No one who has ever seen aggregations of approximately a thousand of the latter gastropod, weighing as much as 15 pounds each, would doubt that these great slugs are the predominant animal in the

region observed. Yet neither of these gastropods is confined to a particular region, for they migrate a considerable distance. In general, then, our picture of the community of the slough is further complicated by the surface animals, some of which remain fairly constant in a particular neighborhood, others that migrate considerable distances. The scope of their influence upon the underground population is negligible. A dominant animal on the surface, therefore, can not be dominant underground, and, conversely, a dominant animal underground can not be dominant on the surface, though some of the underground animals exert more influence on the surface, for example, *Callianassa*, than do most of the surface animals on the substratum.

A dominant form in a particular locality may be, and often is, dominant only as long as its life span. This is because upon the dying out of the dominant of a particular region, due to old age, or other causes, it may be replaced by its own kind or it may be replaced by another dominant. Here again it is necessary to know the life history of the animal. The main factor which determines the dominant animal thereafter will depend upon the set or settlement of a larval brood at a propitious time. This I have discussed at more length in another paper (MacGinitie, 1938, pp. 212-213).

Just how one should delimit a community in the mud flats, then, it is impossible to say with our present ideas regarding animal communities. In my work on Elkhorn Slough it was possible to combine the entire region into a single account because I not only investigated thorouoghly the surface forms, but also a very considerable portion of the slough bottom to a depth of two feet with a shovel. If we were to adopt a more uniform concept of what constitutes an animal community, then perhaps the answer to such questions would not be so difficult. As the situation now stands, a review of most of the sociological papers on marine animal communities shows that every writer has his own opinion of what constitutes such a community, though, of course, it must be said that there is a general agreement regarding such concepts. On the whole, wherever possible, I think the locality should be used to name a marine community. Too, from what has been said, it is evident that the idea of dominance is not very important in estuarine regions.

One other fact that I should have mentioned, and which is of great importance, is that among these scattered communities, colonies or aggregations of dominant type animals one finds many areas of a size equal to those occupied by dominants, but in which there is no indication of a dominant of any kind (MacGinitie, 1935, p. 657).

Ocean Bottom Communities

On the same type of bottom off Newport Bay one may find communities of the holothurian *Stichopus*, the asteroid *Astropecten*, the echinoids *Lovenia* and *Lytechinus*, the hermit crab *Paguristes*, the gastropod *Kellettia*, and others perhaps not so definite. Here we are confronted with definitions again. Are these communities or aggregations? Although I have no proof for the statement, I am quite sure that there is also a tendency for many of these forms and others to segregate more closely when mating time

approaches. On the ocean bottom, then, we have the same situation that we have in the estuarine regions such as Newport Bay or Elkhorn Slough, that is, the botom is spotted with aggregations or communities of surface animals, and over a period of years these spots change, that is, animals change places. That the same condition exists on the east coast is shown by Allee (1934, p. 548), quoting the naturalist Mr. George Gray. However, he fails to note that these communities are not permanent, but that they may and often do change places over a period of years.

From nearly six years of dredging activities I feel that the same thing is true of the ocean bottom as is true of the estuarine localities, that the burrowing forms also are segregated into communities or patches having their so-called dominants as exemplified in the estuary by *Phoronopsis, Callianassa, Schizothaerus,* etc. An advantage which I have at Newport Bay is that, following what we call Santa Ana winds, which occur two or three times per season, one can see the bottom very well with a water glass to a depth of 30 feet or more. Knowing the signs of the burrowers as I do, I can thus get a very good picture of the bottom to that depth. I have found that the same conditions hold that I have described for the shallower regions.

The bottom communities of Petersen (and note that they were called bottom communities and accepted by ecologists as such) are groupings mainly of surface animals which are not by any means climactic communities, and which were capable of change due to migration, replacement by others, etc. The burrowing forms which he lists in his communities are shallow burrowers, and the deeper animals are entirely left out. From the evidence I have given, it is obvious that these deeper forms which were omitted are the so-called dominant forms of the substratum.

From the evidence furnished by such regions as Newport Bay and Elkhorn Slough, which can be termed portions of the ocean bottom drawn inward and subjected to tidal exposure, I am of the opinion that no survey yet made of the ocean bottom outside has more than approximated a true picture of the animal communities found therein. I have had many years of experience with different forms of samplers and dredges, but I have yet to find one or a combination of several which will provide one with a satisfactory picture of the animal life of the smooth bottom of the ocean. Petersen's sampler, and others of this type, do not penetrate sufficiently deep to get many of the animals that I know must be there. At the Hopkins Marine Station at Pacific Grove we built a modified Petersen's grab for Dr. Skogsberg to use in his hydrobiological investigations. Comparatively, this grab was fairly efficient. However, when a grab of this kind settles on the ocean bottom, many of the animals, crustacea in particular, escape because of their activity and efficient movements. In the smooth mud bottom of the ocean, where grabs of this type seldom if ever penetrate more than four inches, the greater bulk of the animals are not taken. The grab just mentioned would take molluscs such as *Nucula, Leda,* etc., which live just below the surface, but it never took many of the larger clams, which I feel certain are there, but which can withdraw their siphons to a depth of 12 inches or more. Neither does it take many such burrowing

forms as shrimps, stomatopods, worms, etc. It does, however, take the tops of tubicolous worms, and the numbers of the ends of such tubes give one an idea of the abundance of the particular species involved. I know of one stomatopod in the smooth bottom off Newport Bay, California, which, I am quite sure, is fairly abundant, yet which would never be taken by such a sampler. It is large and active and makes a burrow about an inch and a half to two inches in diameter, and this burrow extends to a depth of 3 or 4 feet. These creatures are exceedingly efficient predators and must exercise considerable influence upon their associates. If there are such animals on the smooth ocean floor as *Upogebia, Callianassa, Urechis, Schizothaerus* and *Panope,* animals of a type which I have every reason to believe are there, they probably never would be taken by a Petersen grab.

Dredges, of course, from their very nature, penetrate less deeply than do the grabs. If some kind of raking device is placed in the mouth or before the opening of the dredge it will stir up the mud to a depth of a few inches, but in such a case many of the livelier forms escape, so we have no true picture of what the animal population on the surface is. I think the most efficient of all surface samplers is the dredge-trawl. After using an ordinary dredge for a long time, and getting fairly uniform samples, one begins to feel that the dredge must be rather efficient, but when one compares a dredge haul from the same region with that of a trawl haul, he finds the differences startling. The efficiency with which the trawl picks up many of the swift moving animals at once convinces one of the inefficiency of the ordinary dredge. However, the trawl fails to take the smaller life, which is just as important in obtaining a true picture of what is there.

Until we can have apparatus sufficiently expensive to obtain samples from the bottom of not less than a square foot two feet deep, and in combination with the trawl, can we be even approximately sure of the animals which constitute the burrowing communities on the smooth ocean floor. I do not mean in the least degree to depreciate the work which has been done by such boats as the "Albatross," "Challenger," etc., but I do claim that their dredge hauls are only partial pictures of the actual community represented.

It is possible that the deeper the water the shallower the burrowers go, but we have absolutely no evidence to support such a view. Of only one thing can we be certain, and that is that where the bottom is covered by a layer of soft ooze 6 inches or more in depth there will be no burrowing forms, and a layer of ooze less thick than this will exclude most forms. Recently while visiting at the Bureau of Fisheries Laboratory at Pensacola, Florida, Mrs. MacGinitie and I found, washed up on the Gulf beach, portions of a gaper shell which shows that somewhere offshore a clam weighing 4 or 5 pounds has established itself, but which, so far as I know, has never been taken. I also know of two occasions in which heavy surf has brought in great numbers of large bivalves which were absolutely unknown to that region before, although extensive dredgings had been done in both localities One of these instances was at Pacific Grove, near the Hopkins Marine Station, where large *Saxidomus* were washed in by a heavy surf, a surf sufficiently heavy to wash boulders weighing two and three hundred pounds across the highway bordering the

shore. The other instance was at Huntington Beach, California, where large numbers of the clam *Amiantis callosus* were washed in during a heavy surf. In this latter region we have made rather extensive explorations with the laboratory boat and dredge, but never obtained this clam. I cite these two examples only to illustrate the fact that I am sure the fauna of the burrowing forms of the smooth bottom of the ocean are not sufficiently known in any case to warrant making complete community pictures.

On the ocean bottom, as is the case in the estuaries, the surface communities are, in general, composed of shorter lived animals, the majority of which are able to migrate. The burrowing animals have a longer life span, and are more uniform over a number of years, but, as has already been pointed out, considerable change must occur with the dying out and the subsequent settling of the same or new animals.

At the Kerckhoff Marine Laboratory we make considerable use in the summer time of the sea urchin *Lytechinus anamesus*. Sometimes it requires a week of dredging to find a colony of these urchins, but when one does locate them, a short dredge haul will often yield several bucketfuls. In returning for a new supply within a week, one can be fairly sure of finding them at approximately the same place; but if a month elapses several dredge hauls will be necessary before they can be relocated, and they may have migrated in any direction. So far, however, there is evidence that they are found only from one quarter to one mile off shore. The exact limitations, of course, are not known, as it would take months of dredging to find the answer to one such simple question. Another indication that I have of the spotted condition of the ocean bottom has been gained by making numerous trips with a lobster fisherman who sets his traps in the summer time on the smooth bottom for bass. At one spot the traps will be nearly full of the large snail *Kellettia kellettii*, at another of the hermit crab *Paguristes bakeri*, at another of the cancer crab *Cancer anthonyi*, etc. If, as the evidence indicates, we have the same conditions on the smooth bottom outside that we have in the bays, then the same conclusions also hold, that is, that the different dominant animals are scattered in patches. That I am not alone in my opinion that the community idea has been overworked, at least in the smooth bottom areas, will be seen by reading Die Assoziationen der marinen Weichböden, by Arne Lindroth (1935), and the following quotations from letters received from Dr. Lindroth and from Dr. Otto Linke, respectively:

> I have read your paper "Ecological Aspects of a California Marine Estuary." Thereby I was highly interested in your view upon the association and zoning problems. As I have worked in marine sociology myself and even published a paper expressing my disbelief in associations, I thought it would perhaps interest you to have this paper and see how I have been forced to the same standpoint against association making as you have.
>
> Also I can not affirm for the North Sea tide flats a distribution of zones, but always only a distribution in individual associations that will not remain constant, but which at times will change or entirely disappear and will be replaced by entirely different associations. I am inclined to call these groups associations, if one does not connect with the name of associations the possibility for self regulation as in the greater biotic zones. I should be glad if you would tell me how in your work you

interpreted the meaning of association. In my opinion one can speak, at least in the tide flats, of associations. (Translation from Dr. Linke's letter.)

The communities thus far described are transient affairs on the surface, and, though the underground animals are more stable, they are seldom made a part of such community reports. Also, the surface and subsurface communities are separate entities, having but little influence one upon the other.

Rocky Shore Communities

The sessile communities of the rocky regions compare favorably with the burrowing forms of the smooth bottom as regards their stability and uniformity over a longer period of time, but they are by no means so unchanging as one would be led to think by most papers on marine animal communities. On the rocky beach a continual succession is exhibited in portions of rocky shore habitats that are constantly being partially or wholly denuded of their animal populations. These areas may be quite small or sometimes rather extensive. They may be caused in many ways: by floating objects, by storms and floods, following which fresh water dilution may kill the animals, by unusually heavy surf, by the animals piling up on one another until the surf breaks them loose because of the weaker link of dead material below the living, by age limits, etc. In Southern California we have a continual succession in the mussel beds due to the activities of the predacious starfish, *Pisaster ochraceus* (MacGinitie, 1938a). These factors vary in different localities, for example, under the head of floating objects one may mention that on portions of the Scandanavian coasts the ice denudes the rock yearly, while in Southern California the effect of floating objects is limited almost exclusively to a wreck of some kind. It is the succession which follows a denuded area in a mussel bed that made Hewatt's paper (1935) of so much value.

In the rocky region there is not the necessity of considering the free-living animals as migrants that there is on the smooth ocean bottom because practically all of the free-living animals of the rocky region have their own particular hole, crevice, or other spot of refuge from which they sally forth on foraging expeditions. Because of the competition for space due to the great abundance of animals in the rocky region (which, in turn, is due to the refuge the rocky region affords), and also due to the necessity for refuges from tidal exposure, it is necessary for the animals of such a region to have and to hold a place they can call their own. Those which do not, such as, for example, some of the snails, migrate but short distances. This is true for two reasons, first, that most of them feed on the surface film of algal growth covering the rocks, which makes it unnecessary for them to move any great distance, and, second, that in rocky regions there are usually frequent barriers which tend to prevent migrations except for short distances. And so, therefore, the free-living animals of the rocky region show much less change than do those of the relatively smooth bottom of the estuary and ocean over an equal period of time.

In rocky regions, and to a lesser extent on sandy beaches, certain animals occur in strips in relation to the tide. When such is the case, it means that delimiting communities is not at all difficult. But if we disregard mussels and

barnacles, the animals in the remaining regions show much less indication of close segregation. Therefore, dominant animals are not so conspicuous in this remaining portion of the rocky littoral, they are less so in the estuaries and bays, and become practically non-existent on the smooth bottom outside.

Because of this occurrence of some animals in strips, much has been said and done regarding zonation, and I feel that we should pay it some attention at this point. On the whole, it has, I am sure, been decidedly overdone. When Hewatt began his work on the strip of rocky beach at the Hopkins Marine Station (1937) I predicted that he would find three definite zones and no more. This turned out to be correct. These three zones were (1) a high tide zone, where certain animals have become adapted to a considerable tidal exposure, some even being practically free from their salt water habitat; (2) another zone in which many animals have become adapted to the ordinary run of tidal exposure; and (3) a third zone beginning at low water, where tidal exposure is seldom experienced by the animals, and, if this does happen, it is for a short time only.

Among those animals which inhabit the first zone we find barnacles and limpets predominant. In the second zone we find the mussels, but the mussels are limited to a facial exposure on the rocks where the tidal zone meets the breaking surf. Hewatt (1937) used a strip of rocky beach 108 yards long and one yard wide. Of this strip not more than the last 5 yards were given over to the mussel community. From this I think it is evident that both barnacles and mussels are, to a considerable extent, specialized as far as rocky littoral is concerned, and, therefore, are not to be justly defined as being most typical of this region, and certainly they are not typical of any other littoral regions. It can be said of the mussels, however that they harbor beneath them many typical rocky intertidal forms, and, therefore, the animals beneath the mussels are more typical intertidal animals than the mussels themselves. If the mussels were left out, the mussel bed community would then be a fairly typical intertidal community. Again, then, I say, so much for the idea of dominance. I think it is much better to use a larger area to delimit a community, because using mussels or barnacles as dominants in delimiting a rocky shore littoral community is like using the dominant shrub in the border where trees begin as the dominant plant of a forest. In the greater part of the remaining region, where the barnacles and limpets are more evident and predominant, these creatures are specialized in that they can close out the surrounding air and prevent desiccation, can stand a considerable range of temperature, and are not dislodged by the surf. The typical animals of the region, however, are those which live somewhat lower, and which, when the tide is out, hide in the rocky crevices or under the seaweed.

It is much better to obtain a picture of the rocky littoral as a whole than to do specialized parts of it hit or miss. Specialized problems can now be referred to Hewatt's paper, and it is only after one has done such a piece of work as Hewatt did that he is capable of passing on the merits of specialized problems which relate to such a region. Unfortunately, the general concept of marine communities in rocky habitats has been derived mainly from persons

whose work has been superficial, if it has been done over a long period of time, or from the reports of people with little or no background who have done a summer's work at the seashore with little idea of what takes place over a longer period of time.

Sandy Beach Communities

In the sand beach communities on the coast of California the numbers of species are rather limited, but the numbers of individuals of a species are sometimes exceedingly great. What has been said concerning the relatively slow rate of change among the burrowing communities of the smooth bottom applies even more strictly to the dwellers on the sandy beach. Because of the conditions on the sandy beach, we have only burrowing forms there. When unmolested by man, the sandy beach community reaches a condition which is more nearly climactic than that of the rocky shore or the estuarine bottom. Other than the renewal of lost numbers, there is little evidence of succession over a period of many years.

The *Emerita* community, with which I am more familiar, offers a very fine example of a sand beach community (Weymouth and Richardson, 1912; MacGinitie, 1938b). Emeritas occur in such great numbers that on a gently sloping beach I presume they make use of a goodly proportion of the food available on the beach between high and low tide mark. By the time the break flows down the beach over a bed of Emeritas 15 or 20 feet wide, with these animals so thick in the sand that one can hardly push his finger into it without touching a crab, there surely must be little microscopic material left after they have combed it for food. Therefore, the associates in an *Emerita* colony consist of a few predacious feeders and a few scavengers, for always in such a large number of animals with a fairly short life span there is a considerable mortality constantly going on. Two animals in an *Emerita* colony which depend almost entirely upon the dying members of the crabs are the spiny sand crab, *Blepharipoda occidentalis,* and the isopod *Cirolana linguifrons.* Since the isopod is tiny, it occurs in great numbers, and it is almost impossible for one to stand still barefooted in a bed of Emeritas because these little scavengers begin eating on one's feet, and each bite is like the prick of a needle. Though it is exceedingly abundant, this little isopod is considered rare, which shows the lack of study of the life of sandy beaches.

Size and life span have a great deal to do with the associates in a sand beach community, for, by comparison, in a bed of Pismo clams the amount of dead flesh is much less than in an *Emerita* bed. The clams are fewer in number, and their life span (Weymouth, 1923) is at least three or four times as long as that of *Emerita.* On a steep sandy beach the width of an *Emerita* colony with reference to high and low tide is very much narrower, sometimes not exceeding more than three or four feet.

In areas where *Emerita* colonies are absent, one finds the isopod supplanted to a great extent by mysids, which are able to sift their own food from the water as does the sand crab.

Farther north along the Oregon and Washington coasts neither *Emerita*

nor the Pismo clam is found, but on the gently sloping, well-compacted beaches the razor clam, *Siliqua patula*, is abundant. Actually, the food conditions are better on the northern beaches than along the California coast, but, perhaps due to the heavy surfs of winter, it is only on favored beaches that even the razor clam can exist. The steeper sandy beaches are practically devoid of life.

In a wave approaching shore before it breaks, a particle of water moves in an ellipse, but, after breaking, the top portion of the wave is carried up the beach. This causes a more or less steady current of water from the surface next the shore up the beach, then down the beach and along the bottom. And it is this current flowing in on top and out along the sand which makes food material so abundant between tides on a sandy beach. It not only carries the contained plankton of the upper surface of the shore waters to the animals, but it also carries back from higher up, as the tides come in, certain single-celled green algae and, I am quite sure, a considerable amount of bacteria. The green algae and bacteria are more abundant, of course, on the gently sloping beach.

Just below low water mark, out to a depth of 50 feet or more, is an area which is very rich in food. Animals which have not become equipped to stand the churning of the surf and sand are fairly abundant in this region. Practically all planktonic forms are destroyed in the surf, and, therefore, the region bordering a sandy beach just below low tide is rich in food materials. As has been said, the top part of the breaking wave is carried in shore, but the major portion of the planktonic food is dropped out, as it is only the top portion of the breaker which washes up the beach. One of our most common animals just below low tide mark along sandy shores on the west coast of America is the sand dollar, *Dendraster excentricus*, which occurs in a strip just below the breakers.

Objectives of a Marine Ecologist

What is, or what is to be, the objective of the marine ecologist? It seems to me that, concisely stated, the objective of any animal ecologist is to draw as complete a picture as possible of the life of the animals of a region. This picture should be so organized and presented that, together with plant ecology, it will be the fundamental subscience of biology. It should be the goal, not only of the marine ecologist, but of all ecological investigators to present their material in a concise, understandable way, using a minimum of technical language, and striving to put their information into a shape and form that can be readily used by any of the allied biological sciences. The position of ecology is unique, for, since it is the study of the living animal, it should be fundamental background knowledge, and should be easily available and accessible to any biologist who is pursuing specialized investigation in such fields as physiology, anatomy, genetics, etc. It is no credit to an ecologist to present his results in such a way that but few people can understand them. Anyone can do this, and it may be made to cover a multitude of sins, mainly of omission. But if the ecology of the future is to assume the important place to

which it is entitled, ecological data must be presented in such a way that it can be readily used by any biologist, whatever his field. A physiologist, an anatomist, a geneticist or a taxonomist should not be expected to become an ecologist just to be able to understand the pertinent facts relative to the ecology of a particular animal.

Those who engage in ecological research have, therefore, great need of uniformity of methods and concepts. May I suggest the following requirements for marine ecological research?

1. Marine ecological workers should have ample training and background in their subject, or should do their work under the supervision of someone who has such a background. It takes just as many, or more, years for an investigator to develop sufficient background correctly to read and interpret the results of investigations relating to natural history as it does in any other branch of biology. Ecology is a comparatively young division of science, and so some excuse may be made for inexperience, but until this condition is recognized and remedied, ecology and ecological papers will be received with skepticism and be justly criticized and ignored by the followers of biological sciences in general. Often students at marine laboratories are given so-called simple problems in natural history, and later many of their results find their way into scientific publications. The student does something with practically no background, and the paper is too often passed upon by instructors whose background is also insufficient to judge correctly the merits of the student report. The importance of long time experience is shown by Allee's Studies in Marine Ecology (1923), in which 18 staff members and about 400 students engaged over a period of 8 years. On page 189 of his paper Allee makes this statement: "With growing experience in collecting each year we have broken previous records with monotonous regularity for number of species from most of the localities we visited." In the same paper he also notes that animals may be found out of their range and he apparently thinks that if collecting were to continue over a long enough period that almost every species would be found in every locality. I am in full accord with this experience of Allee's, but again I contend that when the life histories of the individuals are known we shall know when they are out of their natural habitat.

2. The main laboratory of the marine ecologist should be the field. The man-made laboratory should be used and equipped in such a way that the field may be reproduced as nearly as possible. It should be accessory to the field. Experiment is investigation under artificial conditions, and, if it is to be efficient, it should follow, not precede, field work.

3. Marine ecological workers should be exceedingly careful to arrive at the truth and to know that their records show conditions as they exist naturally in nature. Carefulness on the part of an ecological investigator is possibly more important than in any other allied biological science, because nowhere will variation be more manifest, and, therefore, nothing should be taken for granted.

4. Ecological workers should be supplied with a goodly proportion of com-

mon sense, for in making their selections for the study of communities they must be able to choose and to eliminate in such a way that when the task is done it will represent a true cross section of that particular community.

5. Such workers should have access to the reports of, and be acquainted with the work of others in their field. So much for the investigator.

Major Benthal Divisions

The primary divisions of the marine environment, as arranged by Hesse, Allee and Schmidt, I highly recommend as being most convenient and usable. Therefore the suggestions here made apply only to the benthal habitat. This I think can be conveniently subdivided into:

1. The ocean bottom
   a. The rocky bottom
   b. The smooth bottom
   c. The estuarine bottom
2. The rocky shore
   a. The high tide zone
   b. The mid tide zone
   c. The low tide zone
3. The sandy shore
   a. An upper region corresponding to the high tide region
   b. The region from there to the lower limit of the breaking surf.
4. The Pelagic

The divisions of the rocky shore should be held to not more than the three main regions or zones listed above. The high tide zone extends beyond the region of high water, and the low tide zone extends to the lowest water mark, that is, to a point where the action of the surf does not affect the inhabitants to any great extent.

The Community

The first problem is to determine what constitutes a community, that is, to delimit or set boundaries. Such boundaries are usually indicated by certain natural conditions or set of conditions of the environment. Here we meet with a fundamental concept, and, in contrast with the determination of the chemical constituents of the water, which is simply a matter of routine, the worth of a study of an animal community depends upon the judgment of the person engaged in the research. I know of no way of making any hard or fast rule for determining the limits of a community other than the good judgment of the investigator. I notice that Cain and Penfound (1938) are in agreement with this idea, for, to quote (p. 401): "Sociological statistics should not be followed slavishly. There is no substitute for good judgment in such matters, and good judgment, of course, implies experience." About the only generalization that would perhaps be of any worth would be that an animal community should be limited to a region where the general conditions and the bulk of the food are approximately the same for the region which is considered to support a particular animal community. It should be thoroughly understood that there are no two environments exactly alike, and, to a greater extent, no two communities alike, because, since the environment is the sum

total of all of the external factors which affect an organism, it follows that organisms affect each other, and, therefore, in this way make the environment more radically different. How they affect each other is determined only by studying their individual natural history.

Occasionally marine communities are found in such condition that it is quite obvious what should be made the limits of such a community. This, for instance, could be a rock of a few hundred square feet in extent jutting up from the ocean bottom, in other words, a small submerged island. In general, however, such limits are not found, and the only way in which they can be determined so that the work will have meaning is through the good judgment of the person doing the work. Dominants are not always possible delimiters of a community. Shelford in his Laboratory and Field Ecology (1929) states that dominants are determined on the basis of size, weight, abundance and influence. I think I have shown that size, weight, and abundance are not always safe evidence for determining the dominant qualities of an animal. I know of no other way of determining the influence that an animal may exert except to study its natural history. Therefore, I feel that no one may classify an animal as a dominant until he or someone else has studied its natural history. It is particularly important to know the developmental history.

When a region has been carefully selected for investigation, the first recordings should be those of the physical and chemical data relating to the community. Since these are easily obtained, they should be complete, and simply and concisely stated. Since physical and chemical data are easily obtained and make a nice showing on paper, they have often obscured the real purpose of an ecological investigation. Here is an instance where a technical presentation may be, or has been, used to cover the sins of omission. However, the physical and chemical factors are only an adjunct to the real purpose in hand.

After the limits of the region have been determined, and the physical and chemical data listed, one should then proceed with the sampling, counting, and listing of the animals. When this is done it gives a check on the area selected for the study, and, quite often it will be necessary to change the original limits to conform to the representative display of animals present.

The name of a community may be given either as representative of the predominating members of the community or for the locality in which they are found. I think that it is safer to use the locality, as very often with marine communities the predominant animal may be predominant in two or more different localities. This was shown by the comparison of the three *Mytilus* communities and by the discussion of the estuarine bottom and the smooth ocean bottom.

After this much has been accomplished the intimate life histories of the evident or more predominant animals should be studied. This is very necessary, for how can one even guess at the influence exerted by any member of a community unless its life habits are known?

It will be noted that I have mentioned many times in this paper the importance of life history work on individual species as an important adjunct of

community investigation. I do not mean by this that other means of distinguishing communities, such as weight, abundance, etc., are not important and that they should not be used to their fullest extent, but I do contend, and I am entirely convinced that no study of a marine animal community is complete until the natural histories or life histories of at least the more important members of the community are known. The ideal situation would be to know the natural history of all members of the community. And do not let it ever for a moment be thought that individual life history work is more easily obtained than that of the other criteria, or that to record correctly the natural history activities of any animal species does not require a background on the part of the investigator equal to or greater than that of an investigator in any other field. This applies equally to any instructor who is to sponsor any such work done by students.

Again to quote from Cain and Penfound: "It is obvious from previous work (see especially reference to papers by Lippmaa and Cain) that the best method of studying a phytocoenosis is to study the synusiae separately and, on a basis of this knowledge, to synthesize a picture of the association." This seems to me to indicate that neither are the plant ecologists satisfied with looking into the large end of the horn, but that they want to know something of the parts that make up the whole.

In time, life history work impresses upon one the importance of viewing one's results from an entirely impersonal point of view, that is, of striving to eliminate entirely human experience and feelings from one's results. Marine animals are purely instinctive or mechanistic in their reactions. There are no doubt reflexes and responses made by them which are entirely beyond the ken of human experience. The importance of such facts as these are realized only after years of intimate study of particular species.

In conclusion I should like to quote from a paper, entitled The Scripps Institution Pier as a Marine Observatory, by Professor Allen, in which he says: ". . . I hold to the view that the way to learn about anything is to go to it directly, get as much contact with it as possible, and study it as much as possible in the conditions of its natural existence."

Summary

1. Clearer, more uniform, and simpler definitions are needed in ecology.

2. Marine animal communities are anything but static affairs.

3. Variation is the most important principle in ecology, and should be emphasized rather than made subordinant. Animals can not be pigeonholed under unit factors.

4. No apparatus yet used is sufficiently efficient to provide a complete picture of ocean bottom communities.

5. Free-living animals migrate greater distances on smooth bottom than on rocky shores.

6. Sand beaches provide habitat for burrowers only.

7. Sand beaches are rich in food because of the plankton destroyed in the breakers and because of the green algae and bacteria growing on the moist sand between tides.

8. Marine communities are subject to change through cataclasm, migration, old age, and larval settling chance.

9. Dominance, while apparent in some rocky shore communities, fades out into insignificance in estuarine and ocean bottoms unless smaller regions are used, and even then it is necessary to separate the surface from the burrowing forms. If these two things are done, it minimizes the importance of environment.

10. Using the locality, rather than the generic names of animals, for naming a community is recommended, for dominants show so much variation that generically named communities lack uniformity. Dominants may be dominant in entirely different communities, and their use to name a community may cause the worker to make very small community areas.

11. Background on the part of the worker is shown to be more important than in any other branch of biology.

12. Individual life histories of members of the community are absolutely necessary to a fuller understanding of the sociology of marine animal communities. Every animal is a part of the environment of every other animal in the community, and therefore, is a part of the environment of the community.

REFERENCES

ALLEE, W. C. 1923—Studies in marine ecology. I. The distribution of common littoral invertebrates of the Woods Hole region. Biol. Bull. **44**(4):167-191.

———1934—Concerning the organization of marine coastal communities. Ecol. Monographs **4**:541-554.

ALLEN, WINFRED EMORY. 1933—The Scripps Institution pier as a Marine Observatory. Scien. Month. **37**:371-375.

CAIN, STANLEY A. AND WM. T. PENFOUND. 1938—Aceretum rubri: the red maple swamp forest of Central Long Island. Amer. Midl. Nat. **19**(2):390-416.

COE, W. R. AND W. E. ALLEN. 1937—Growth of sedentary marine organisms on experimental blocks and plates for nine successive years at the pier of the Scripps Institution of Oceanography. Bull. Scripps Inst. Ocean., tech. ser., **4**(4):101-136.

ELTON, CHARLES. 1927—Animal ecology. The Macmillan Co.

GISLEN, TORSTEN. 1929—Epibioses of the Gullmar Fjord I. Kristinebergs zool. stat. 1877-1927. No. 3, 123 pp.
———1930—Epibioses of the Gullmar Fjord II. Ibid. No. 4, 380 pp., 6 pls.

HESSE, RICHARD. PREPARED BY ALLEE, W. C. AND KARL P. SCHMIDT. 1937—Ecological animal geography. John Wiley & Sons. 597 pp.

HEWATT, WILLIS G. 1935—Ecological succession in the Mytilus californianus habitat as observed in Monterey Bay, California. Ecology **16**(2):244-251.

———1937—Ecological studies on selected marine intertidal communities of Monterey Bay, California. Amer. Midl. Nat. **18**(2):161-206.

KING, L. A. L. AND E. S. RUSSELL. 1909—A method for the study of the animal ecology of the shore. Proc. Roy. Soc. Edinburgh. **17**(6):225-253.

LINDROTH, ARNE. 1935—Die Assoziationen der marinen Weichböden. Zool. Bidrag fran Uppsala **15**:331-366.

MACGINITIE, G. E. 1935—Ecological aspects of a California marine estuary. Amer. Midl. Nat. **16**(5):629-765.

———1938a—Notes on the natural history of some marine animals. Ibid. **19**(1): 207-219.

———1938b—Movements and mating habits of the sand crab, Emerita analoga. Ibid. **19**(2):471-481.

MOLANDER, ARVID R. 1928—Animal communities on soft bottom areas in the Gullmar Fjord. Kristenebergs zool. stat. 1877-1927. No. 2, 90 pp.

NEWCOMBE, CURTIS L. 1935—Certain environmental factors of a sand beach in the St. Andrews region, New Brunswick, with a preliminary designation of the intertidal communities. J. Ecol. **23**(2):334-355.

PETERSEN, C. G. J. 1913—Valuation of the sea. II. The animal communities of the sea-bottom and their importance for marine zoogeography. Dan. Biol. Sta. Rep. **21**:1-44; Appendix 1-68.

———1918—The sea bottom and its production of fish-food. Ibid. **25**:1-62.

RICE, LUCILE. 1930—Peculiarities in the distribution of barnacles in communities and their probable causes. Pub. Puget Sound Biol. Sta. **7**:249-257.

SHELFORD, V. E. 1929—Laboratory and field ecology. Wms. & Wilkins Co. 608 pp.

———1930—Geographic extent and succession in Pacific North American intertidal (Balanus) communities. Pub. Puget Sound Biol. Sta. **7**:217-223.

TOWLER, E. D. 1930—An analysis of the intertidal barnacle communities of the San Juan Archipelago. Ibid. **7**:225-240.

WEYMOUTH, F. W. 1923—The life history and growth of the Pismo clam, Tivela stultorum. Calif. Fish & Game **7**:1-120.

WEYMOUTH, F. W. AND CHARLES H. RICHARDSON, JR. 1912—Observations on the habits of the crustacean Emerita analoga. Smith. Misc. Coll. **59**(7):1-13.

WORLEY, LEONARD G. 1930—Correlation between salinity, size and abundance of intertidal barnacles. Pub. Puget Sound Biol. Sta. **7**:233-240.

KERCKHOFF MARINE LABORATORY,
CALIFORNIA INSTITUTE OF TECHNOLOGY,
CORONA DEL MAR, CALIFORNIA.

DISCUSSION

Emerson: Apart from the individual life histories, ecologists should also understand the physiology of the organism and its evolutionary history. The further we go the more complex biological processes appear. In attempting to understand complexity we tend toward over-simplification of concepts. Every time a generalization is made, it is an over-simplification. This is not peculiar to ecology but every biological discipline has met the same difficulties. Schools of thought have emphasized one principle and as they analyze and synthesize their material they find their borderlines indistinct and related to other fields. At the same time they have to expand in order to understand better the things upon which they are working.

MacGinitie: Although I am very much in accord with such statements I still feel that the study of the community should be presented as simply and directly as possible;

beyond that, it will be the concern of specialists in the field of ecology. Since any organism may be the unit of ecology, I stress the individual natural histories.

Mottley: Cornell has been the home of this point of view and I am extremely interested in it. There is, however, more to ecology than just that. The life history and natural history of each organism in the region of study must be known. This knowledge, which is backed up by experience in the past, is used to predict what is going on now in a community. Knowing the natural history of all the organisms of a community can one predict what it is going to do tomorrow?

MacGinitie: Yes, to a very great extent. By synthesizing these facts a fine picture of a community may be obtained. What would be left out by this synthesis of a community?

Mottley: The inability of the human mind to grasp the whole picture is overlooked. Also, there is the question of population, which makes any prediction difficult.

MacGinitie: If the entire picture is considered, this is not true because the population will be known.

Mottley: The whole picture comprises more than the individual members of the population.

MacGinitie: The arrangement or synthesis of these facts must be comprehensive and nothing should be omitted.

Emerson: If we start with the simplest expression of animal life, such as the amoeba, we find the complexity so great that the human mind is incapable of grasping it in its entirety. We have to accept that limitation and do what we can. It is a limited understanding we come to, not an absolute understanding. This is characteristic of all science.

MacGinitie: That is true, although I think one places perhaps too much emphasis on the physiology, chemistry, etc. of these animals. Therefore, it is necessary to know the life history to give us a more complete understanding.

Emerson: But after analysis, we must also synthesize. Even when we have carried analysis and synthesis as far as possible, we have not reached the end.

Lippmaa: The chief problem in the study of both animal and plant communities is the problem of the delimitation of particular communities. There are two kinds of limits. Some of them are caused by differences in the habitat, for example, the *Ulva latissima* and *Ascophyllum-Fucus* communities of Long Island. The limits between these communities are real. Other limits of vegetation are conditioned by the ability of some species to form patches, i.e. *Oxalis montana, Clintonia borealis, Cornus canadensis* in the *Abies balsamea* association of the Gaspé Peninsula in Canada. No regularity in the distribution of these patches can be found. They are mostly conditioned by chance factors favorable for the successful establishment of the species.

MacGinitie: There is a difference, however, since the conditions of the ocean bottom can not be compared with these patches.

Mottley: Why are communities on the mud bottom supposed to show normal distribution?

MacGinitie: Any particular community shows a curve of normal distribution. But it takes all of these curves to make a whole.

Mottley: In my experience, they do not follow a normal curve.

MacGinitie: If the community study covers a sufficiently large territory the curve will be related to a normal curve.

Carpenter: I am inclined to doubt the possibility to predict the general structural emergence of a community from the autecology of its constituent species. The whole is frequently more than the sum of its parts. I should like to ask about the questionable dominance exerted by mussels and barnacles. The protection which they offer, even though physical, seems to control the other animals present in the community. Is this a

physical influence? A similar effect is found in the forest: The leaves of the forest canopy tend to keep out the light from the floor of the forest with the result that much of the vegetation is excluded. This is a physical effect, but exerts a very strong influence on the rest of the community.

MacGinitie: We have animals which exert a willingness to exclude others by intent, undoubtedly a real influence. Mussels are dominant and thus they are the only creatures in the mussel community exerting great influence.

Carpenter: The dominance exerted in the case of barnacles keeps everything else olt. In both cases the longer they keep others out the more important they are.

MacGinitie: Barnacles occur largely where other animals can not live although there is ample room for them. The mussel occurs only where the shore meets the surf whereas the animals living in the mussel bed are also found on the whole rocky flat. Dominance is a very useful concept but it is frequently abused.

Carpenter: Can two communities have the same ecological structure?

MacGinitie: As far as I know, no animal communities have the same structure although mussel communities sometimes show similar structure.

Cain: Do marine communities exhibit retrogression due to their own reaction and not due to destruction from some exterior source?

MacGinitie: This can not be called retrogression over a long period of time, because what succeeds a community may be much better. Sometimes the community will be an entirely different one. There are in the ocean, and I am quite sure of this point, many cases, particularly on the smooth bottom where things happen to be propitious for settling of a new community. A fine community, a segregation or aggregation of a particular species may be established there and exert such an influence that it will be dominant. However, there are many marine animals which have the same ability. Sometimes in the case of mussel the place would be covered with barnacles. The mussel can smother the barnacles out. The first to come establishes itself. Often they establish themselves and then another which comes in can make use of the conditions produced by the first until the struggle begins what community it will be.

Cain: That community which is climactic is a large mosaic and any particular aggregation is a temporary thing, living in continual flux. It is comparable to Clements' large association in botany, climactic in a very broad sense and almost infinitely variable.

MacGinitie: That again depends on the concept of the community. I prefer to use larger areas and to name the community for the locality.

Eggleton: Were the terms life history and natural history used synonymously? Is the life cycle of an individual organism more important in ecological study than some of the general phenomena usually called natural history?

MacGinitie: It seems almost necessary to use these terms jointly because in zoology life history refers to the embryological development of animals and natural history is too often limited to the life of an adult animal in a particular environment. Natural history should include both since it is just as important to know the environmental influences on the larval stage as on the adult. My own definition of natural history would include the life of the animal from the beginning of its existence until its death and all of the things affecting it during its lifetime.

Eggleton: Is the susceptibility of an organism during certain phases in the life cycle of the individual a more important ecological factor than feeding, hiding, and the like? The phenomena of emergence in fresh water would show that particularly well. This factor in the life cycle of the individual changes the picture considerably. Those organisms which spend all of their life cycle from egg to adult and back again within the water offer greatly different points of susceptibility than do those which change from one medium to another at some point in their life cycle.

MacGinitie: By knowing its natural history, as I defined it, all of those things would be brought to light.

Fresh-Water Communities

Frank E. Eggleton*

Introduction

There are two fundamentally different concepts of the interrelationships of organisms and their natural environment which have influenced ecologists. One concept lays emphasis upon the habitat as an environment suitable for occupancy by certain organisms. This might be called *habitat ecology*. The other conceives of the associations or communities of organisms, which live in such parts of the lithosphere or hydrosphere as are more or less favorable to their needs, as the essential nature of our subject. This has been referred to as *community ecology*. Each concept has its loyal adherents. It does not follow, however, that all those who labor under either banner would themselves be willing to accept our verdict whichever way we might classify their work. Nor is it to be supposed that these two divergent approaches to a study of organisms in relation to their environment represent all the ways in which ecologists have approached their subject. There are still other shades of emphasis, many others, but with these we are not here concerned, however worthy or profitable they may have proved to be.

It will, no doubt, be readily granted by all that a detailed knowledge of the habitat is essential to an intimate understanding of the behavior pattern of the organisms living within its boundaries. Living things behave as they do in response to stimuli. And probably no one would seriously question the desirability, or perhaps even the necessity, of the ecologist knowing all that he may concerning the nature and magnitude of the stimuli arising in or from the external environment. That these stimuli are diverse, exceedingly variable both in time and in space, intricately interwoven with the very fabric of life, sometimes inadequately measured, often improperly emphasized, and almost certainly never perfectly appreciated as they relate to organisms does not justify neglecting them on the one hand nor warrant their over-emphasis on the other.

Ecology has been often and variously defined. One definition which has at least several virtues describes the subject as *the science which treats of the interrelationships of organisms with their complete environment*. Whether one is considering the individual, the species, or the community there are always three great categories of environmental factors which together make up the composite whole. These three types of factors which together make up cal, and the biological. Together they comprise the complete environment.

The mind of man is finite and quite naturally we must analyze before we can synthesize. Herein lies the real justification for simple environmental

* Contribution from the University of Michigan Biological Station and from the Zoological Laboratory of the University of Michigan.

analysis. By the use of our machines and our procedures we have learned to measure both the quality and the intensity of many environmental factors. We can even arrange to measure several of them simultaneously. By experiment, simple or complex, we study the reactions of organisms to one variable in the environment. We try more experiments varying other factors. We measure, analyze, observe, and experiment and by so doing we gain some knowledge of the behavior of organisms. But too often the idea of the unity of the environment is not with us as we work. No one, unfortunately, has devised an experiment or constructed a machine which will measure all the factors at one time and simultaneously record the reactions of the organisms.

Implicit in the definition above is the concept that the core of the whole matter lies in the interrelationships of organisms with each other and with the inanimate factors of the habitat. Where environmental analysis often falls short is that it omits the effect of organisms as a part of that environment and in particular the indirect effect of organism upon organism. Some factors, by their very nature, affect the whole environment quite as much by their complete absence as by their presence. The complete lack of light or of dissolved oxygen, for instance, exerts a profound effect upon other factors and both directly and indirectly upon the biota. The interplay of these forces is at once the most difficult, the most challenging, and the most important aspect of ecology. The great, monumental contributions to our science in the past have been, and in the future will continue to be, those which exhibit, in some degree at least, a clear appreciation of these complex interrelationships.

That branch of the larger field which deals with the ecology of inland waters constitutes the province of limnology. It has many problems peculiar to itself. In common with oceanography it faces the fact that, very often, observations must be made at a distance. Except at the surface or about the margins it is not possible to collect, measure and observe behavior of aquatic organisms and study environmental factors with the same directness as it is on land. So simple an operation as taking the temperature of the ambient medium requires special types of thermometers or elaborate apparatus for aquatic work. In anything but the most shallow situations it is not possible to observe and collect specimens as one may study and gather terrestrial plants and animals. One must, instead, resort to traps, dredges, samplers and other devices for lengthening one's fingers. These and other considerations have led to the high degree of instrumentation which is evident in the subject today. And in turn this very instrumentation has been at least partly responsible for the trends which the subject has exhibited. It has been one of the reasons why aquatic ecology has followed a path so widely divergent from that which plant ecology, at least in the terrestrial realm, has taken. Different concepts have evolved from different methods of approach to problems which are fundamentally alike. Many, indeed most, of the theories and abstract concepts of the various schools of thought in plant ecology have had little testing and application in limnology.

Although limnology has claimed as its own territory all inland waters,

whether fresh, brackish, or saline, the present paper is confined to a consideration of the problems of fresh-waters. It seems only natural that a subject which, as a distinct branch of science, is younger than some of its leading personalities should still be pondering about its objectives and boundaries. Welch (1935) has stated that he, "conceives the central influence of the subject to be the *problem of biological productivity*." Limnology, he continued,

> may therefore be defined as that *branch of science which deals with biological productivity of inland waters and with all the causal influences which determine it.* This definition does not preclude any of the necessary stress on the different animal and plant communities, since they are the direct result of the biological productivity of waters which they occupy. Inland waters differ to a striking degree in the quality and quantity of life which they contain. To understand the natural circumstances responsible for this tremendous difference in natural waters and to identify and evaluate the influences which govern a particular form of productivity are the aim and province of modern limnology.

Historical Résumé

It is of course true that in common with other divisions of natural science much was known during the days of antiquity concerning some phases of fresh-water biology. However, limnology, as a separate branch of science, has existed for less than half a century. Several men have been proposed as the founder of limnology and prominent among these are Peter Erasmus Müller, Anton Fritsch, F. A. Forel and T. Simony. The fact is, that no one man was the founder of the subject. All these men and many others contributed largely to its early development; Simony with his discovery of thermal stratification, Müller by his early demonstration of the existence of fresh-water plankton, Fritsch through his studies on the lakes of the Bohemian Forest, Forel by his more than one hundred publications dealing with phenomena of fresh-water life, and before any of these the early microscopists Swammerdam, Leeuwenhoek, Réaumur, Trembly and a host of others. Certainly it is true, however, that if any one man can be singled out as being the first one to publish a long series of significant contributions which are truly limnological in character, that man is Forel. Although the first of these early but significant studies appeared about the middle of the nineteenth century, and Forel's first limnological paper was published in 1869, the subject can hardly be said to have become an organized science before the last decade of the same century.

Somewhat paralleling the European record, the first, faint beginnings of fresh-water biology in America consisted largely of work done by the early naturalists during the last half of the eighteenth and the first half of the nineteenth centuries. From about 1850 on great names in American biology appear with increasing frequency in the roster of workers who published substantial contributions to our knowledge of what we now know as limnological phenomena. Of the many only a few can be mentioned, but prominent among them were such men as Agassiz, Leidy, Stimson, Smith, Stokes, Verrill, and Milner. In the later decades of the last century another group of workers began to make further important contributions. Their work continued on into the present century and among them were men known person-

ally by many present today: we many mention Forbes, Kofoid, Reighard, Whipple, Birge, Marsh, Ward, and Needham. From this list of men who must be regarded as prominent among the founders of American limnology, a few have but recently retired from formal academic life and at least two are still at work. Of the men active in the field today nothing need here he said.

Within the first third of the twentieth century limnology has made great advances. Much reconnaissance work has been done and considerable evidence of a virile maturity is becoming apparent. Both abroad and in America there are hundreds of workers studying the phenomena of fresh-water life from many aspects. Their fields of operation include the lakes and streams of every great land mass on the earth. Certain geographic divisions of the world are more richly blessed with fresh-waters than are others and from these regions a large and widely diversified limnological literature is being built at a rate which is constantly accelerating. In the eastern hemisphere there are several nations where groups of workers are contributing constantly. Russia, Germany, Switzerland, England, Austria and Japan are prominent among them. There are smaller but very active groups in Denmark, Italy, France, Poland, Belgium, Hungary, Czechoslovakia, Sweden, Jugoslavia, India, South Africa, and China.

In the Americas, Canada, Brazil and our own country are most active in fostering fresh-water investigations. There are several important centers of activity in this country scattered throughout the nation and hardly a state can be said to have no limnological work in progress within its boundaries. Canada, with her thousands of lakes and innumerable streams is actively conscious of both opportunity and the need for their adequate study. Brazil is becoming conscious of her fresh-water resources and has an active group of investigations under way, largely maintained by the national government.

It might be supposed that with all this work going forward, the world over, nearly every phase of study possible to fresh-water investigations would be in progress. Such, however, is decidedly not the case. There are many programs which include work on nearly all phases of the environment and others which place emphasis on the various organisms, but the one aspect of the subject which is of most interest to us here at the moment, namely a study of fresh-water communities as such, either do not exist at all or are totally unknown to me. This one fact has largely determined the treatment of my subject and the tone of this paper.

Fresh-Water Habitats and Their Biotic Communities

Fresh-waters, although vastly less extensive than marine are world-wide in distribution. The problems of their biota are likewise, therefore, cosmopolitan in distribution. Polar, temperate, and tropical lakes offer the greatest possible range in ecological features. Altitude as well as latitude plays an important role in determining diversity of aquatic environment and high mountain lakes and streams present an ecological picture so markedly different from that which obtains in the plains and lowlands as to render them totally dissimilar in many important respects. Dimensional variations of the

water masses, likewise, further increase the diversity. The biological problems within our five Great Lakes are almost as different from those of the small lakes, ponds, and bogs as are those of the ocean or even the land. Diversity of fauna and habitats is one of the most marked characteristics of fresh-waters.

Quite naturally, this diversity has resulted in the proposal of many systems of classification of fresh-water habitats and their biotic communities. Several European and a few American centers have put forward varying schemes. A few have been based upon what are essentially the supposed dominant animal or plant communities. Others have laid their foundations upon extra-biotic features, the physical or the chemical factors of the environment or both. Most of these schemes of classification have been founded upon a detailed knowledge of the criteria which are evident in a relatively restricted geographical area and to a corresponding degree have failed of world-wide applicability. It is probably not too generous to judge, however, that all of them have contributed to both a better understanding of the great natural diversities existing in these ecological units and likewise to the furtherance of the whole project of arriving eventually at a more nearly universally applicable system of classification. As systems of ecological classification and nomenclature they have in common one great difference from the similar schemes of terrestrial ecology, namely their almost universal failure to apply the terminology and often the concepts which have grown up within the literature of the latter realm. One reads little indeed about *mores, consocies, strata, formations, one-layered communities,* the *biome, climax association* and similar conceptual phenomena in the literature of fresh-water biology. And if I may be forgiven by all concerned for the momentary assumption of the role of ambassador extraordinary, I would plead with those of my colleagues who are devoting their minds and energies so earnestly to the advancement of terrestrial ecology not to judge too harshly when they think on this hesitancy on the part of those of us who work in fresh-waters. Perhaps when aquatic ecologists have more nearly satisfied their curiosity about the phases of limnology with which they have thus far concerned themselves and turn more earnestly to a consideration of the problems of biotic communities *per se* they will find need of the very terms and concepts which they now seem to ignore. On this point, however, I would not be so prophetic as to commit even myself, much less others. Finally may I beg those of you who are of terrestrial persuasion to consider dispassionately two further points; first, the undoubted fact that there is not yet quite perfect harmony of agreement concerning these terms and concepts and their application within your own ranks, and second that they may need radical modification before they really are applicable to aquatic biology. We shall all be able to agree, I am sure, that these things are but the tools of the mind with which we struggle toward that utopian goal, that intellectual mountain peak from whose summit we have been led to believe we may "see life steadily, and see it whole." The very existence of our present conference is both open recognition of our mutual need for a better understanding between the various natural subdivisions of our general subject and a virile and highly commendable determination to do something about that need

on the part of those responsible for its planning and organization. As an individual, I present my personal credentials at this court in a very humble spirit. I seek much more earnestly and hopefully to learn than to instruct. Here I drop my ambassadorial vestments.

Within the ranks of aquatic ecologists there exists perhaps even less agreement as to the details of fresh-water classification than I have imputed to those of terrestrial ecology. But on the major points and in larger categories there is practically universal acceptance. The most widely used major habitat divisions are as follows:

Lotic series	Lentic series	Springs
Brooks	Lakes	Subterranean Waters
Creeks	Ponds	Lotic
Rivers	Bogs and Marshes	Lentic

In such a scheme of classification, the most evident criterion for differentiation relates to currents. Lotic environments are sometimes called the running-water series and lentic situations are referred to as the standing-water series. Under each, the included subdivisions are named in the natural genetic order. Both temporally and spacially brooks become creeks and creeks become rivers. In exactly the same manner, lakes as they age become less extensive and evolve into ponds, and these in turn metamorphose into bogs and marshes. Springs are so varied in their characteristics as to require separate consideration and likewise subterranean waters, which may be either lotic or lentic of course, seem to differ in such degree from their nearest counterparts on the earth's surface that they too merit exclusion from that group of waters.

Fresh-water communities *per se* constitute the special field of this paper. By the term community we here mean those intergraded and interacting aggregations of plants, or animals, or both which are characterized by broadly limited taxonomic composition, distinctly similar physiological requirements, and relatively uniform habitat limits. Under the restrictions of this application of the word there is little in the world's limnological literature which can qualify without reservations. It does not seem appropriate, however, to reframe a definition merely in order to include literature which originally made no pretense of being other than what it is. Much of the work which we shall consider, therefore, would not qualify as community studies even under my own statement of what constitutes that ecological category. Shelford (1918) in discussing animal communities wrote:

> Numbers of animals select the same environment because of physiological similarity. All the animals occupying a relatively uniform habitat constitute an animal community. A physiological agreement exists among the animals of a community. .... There is agreement in reaction to factors of prime importance in the community habitat as a whole and disagreement in respect to factors differing strikingly in the levels in which the animals live within the community habitat.

Our present statement of the application of the word community is seen to be in essential agreement with Shelford's formulation. It is largely due to this point of emphasis that so much limnological work which has been done does not properly qualify as truly community study. The fact is merely this:

few limnologists have purposely set out to study fresh-water organisms from that point of view. They have been exceedingly busy working from other approaches. It seems probable that more and more work will be done in the future in which the approach is definitely planned with the community concept in mind.

Lotic Communities

Lotic communities vary greatly in different types of streams. In intermittent streams, the biota is restricted by the peculiar exigencies of the habitat. Species are few and populations manifest marked fluctuations which follow in a dramatic manner the rise and fall of the water level. Here, in the flood season, the stream bed is often subjected to the same severe erosion and violent molar action which characterizes the torrential streams of mountain areas. Silt beds are often lacking or restricted to the stretches of more gentle slope and in rocky or glaciated regions the course of the stream will afford little shelter for the development of highly organized communities. Among the few animals which are able to withstand the rigors of such a habitat the successful will be those whose life history pattern provides quiescent stages in which the individual can pass the periods of drought or the phenomenon of emergence by which arrangement it would normally be absent in any case from the aquatic habitat during that period when the water level is lowest. A few other forms are those which can withstand the inimical conditions due to the crowding within the small remanents of the pools along the stream bed. These include certain fly larvae like Odontomyia which respire through protected spiracles and derive their air supply through tubes thrust above the surface film. Kuster (1934) has shown that these larvae are able to endure extremely severe conditions such as would be set up by pollution and crowding. Leeches, some of the borrowing Oligochaeta and several Protozoa, live in the mud which gathers scantily in these remanent pools.

One of the most far reaching environmental factors, indeed the most characteristic and powerful one, in lotic communities is current. Either directly or indirectly it profoundly affects the biotic assemblages of streams. The problems of existence are so modified by this one factor as to necessitate separate consideration of the principal types of biotic communities in each of the two major types of streams. Life for the organisms of permanent swift-water streams is vastly different than for those plants and animals which inhabit sluggish ditches, creeks and rivers. In either sort of stream, however, the *types of communities* remain the same, namely nekton, plankton, and benthos. Naturally, the individual communities within each of these three great categories differ widely in the two sorts of streams.

We might outline the major categories of stream communities, then, in the following arrangement.

Communities of intermittent streams
Communities of permanent swift-water streams
  Nekton
  Plankton
  Benthos

Communities of sluggish-water streams
Nekton
Plankton
Benthos

In permanent, swiftly flowing streams the nekton consists largely of fish communities. Ricker (1934) reported that for small, cold, soft-water streams of this type in Ontario the speckled trout, *Salvelinus fontinalis*, was the only fish typically present, but that in hard-water creeks of the same type the sculpin, *Cottus sp.*, and the stickleback, *Eucalia inconstans*, are often present in the fish communities. The ecological classification of Ontario streams offered by Ricker (ibid.) is of considerable interest to us here because he bases it not only on physical and chemical characteristics but likewise in part on the biota. The two major categories of his system are (1) creeks and (2) rivers. The criteria which he used to distinguish between the two were (1) volume of flow, which is of course another way of referring to what we have called current, and (2) average width. The creeks are divided into two types, namely "spring creeks" and "drainage creeks" and the former is further subdivided into four subtypes. In the first instance his criteria are largely the permanence of flow, i.e. intermittent or permanent streams, and the maximum summer temperature of the water. In the secondary kinds of creeks his criteria relate to type of bottom, rate of current, and type of predominant vegetation.

The rivers he also divides into two major kinds on a basis of temperature and volume of flow. In the colder type of river the trout is again the predominant species of the nekton community and in the slower, warmer streams the fish communities are more or less complex associations of species from the Centrarchidae and Esocidae. The trout streams are again subdivided into two types on a basis of current (slow or swift), type of bottom, predominant vegetation and in one instance the predominant invertebrates. A third subdivision under each secondary type divides the habitats into "slow hard waters; slow soft waters" and hard or soft swift waters. The warm rivers are divided once into two types on the basis of character of bottom, rate of current, and predominant vegetation.

The indigenous plankton communities of permanent, swift-water streams are characterized by marked paucity of species and small numbers of individuals. The problems of turbulence in relation to plankton has received scant attention but at least one investigation of the matter is being conducted at the present time. Streams which derive a part of their volume directly from standing waters of any considerable size have their plankton communities profoundly affected by that factor. A similar end result, although a qualitatively different one, is produced when stream waters are impounded. Chandler (1937) found that the total plankton population of a river is greatly augmented by lake components just below the lake outlet, but that this plankton of lake origin soon decreases under typical river conditions. He reported that the quantitative plankton decrease was greatest where vegetation was heaviest and that the decrease was exhibited by "(a) total net plankton; (b) by each large plankton group; and (c) by certain predominant individual plankters."

One of the few outstanding exceptions to the general statement that there

is little in the world's limnological literature which can qualify as true community studies and without reservations, is Eddy's, "Study of Fresh-Water Plankton Communities" (1934). This is an important contribution to limnological literature. It is especially so because of the scarcity of similar papers, but it would still be valuable if there were many others of comparable nature. Several of his conclusions and statements are of such general application and are so clearly formulated that they can be quoted here in whole or in part to distinct advantage. Other sections of his paper have served, in part, as a source of illustrations for my own generalizations.

Eddy states that,

> The plankton element of fresh-water communities consists of organisms whose behavior is comparable in certain respects to that of the organisms of terrestrial communities. Some species which are conspicuous or abundant may be called predominants or prevalents, in the same sense as these terms are used for the abundant organisms of terrestrial communities. Some predominants are perennials and others seasonals. Some predominants are common in all kinds of relatively stable fresh-water communities and indicate an associational and formation-like structure comparable to that of terrestrial associations and formations, in which the predominants are of two classes, those which characterize the particular association and those which characterize the formation and serve as binding species. ....
>
> Some predominants which are seasonal in the early stages of plankton development in a stream become perennials when the stream presents more stable conditions throughout the year.
>
> There is a progressive development of the plankton element in streams comparable to the invasion of the barren area by terrestrial communities. This begins with the first evidence of stable conditions in the course of the stream in summer. Downstream, as the conditions become more stable, there is an increase in the number of species and the abundance of each.".... "apparently, the number of perennials increases as the climax is approached.....
>
> The important factors influencing the development of plankton are age of water (i.e., distance from source ÷ velocity), temperature and turbidity.... other factors such as light, dissolved oxygen, and hydrogen ion concentration seemed to be always sufficient to meet the requirements of the plankton.... a few plankton organisms usually appeared in water 6-10 days from its source, while an abundant plankton appeared in water 20 days or more from its source.

Eddy also concluded that in the waters which he studied, "there are, in general, four types of plankton society which may be characterized by their predominants." One of these is of interest at this point. This he described as follows:

> Rivers and related waters exhibiting some degree of stability: four species of Brachionus, two of Synchaeta, *Filinia longiseta*, and *Moina micrura*.

It has been repeatedly demonstrated that the plankton in polluted streams is often carried not only into but through the regions in which wastes occur. Thus Wiebe (1928) found the upstream plankton of the Mississippi River occurring both in and below the polluted stretches of the stream below Minneapolis and St. Paul. This phenomenon is further complicated, where the stream waters are impounded, by the development of plankton communities with their own characteristic predominant species typical of such slowly moving river waters. Probably nowhere, except perhaps in their lower reaches,

are the plankton communities of streams as complex as they are in the standing waters, and they are typically less abundant both in species and in individuals.

It has been pointed out before in this paper that in every type of habitat the problems of the biotic communities are profoundly affected by many and some times by all the physical, chemical and biological factors of the environment, but it will bear reiteration. Often, however, some few factors, or even a single one, may be of such predominant importance that they exert an influence all out of proportion to their seemingly intrinsic worth. Thus for the bottom dwellers, the character of the substratum on and in which they live is usually of such paramount importance that its effects may completely outweigh the influence of other powerful factors.

In the swiftly flowing streams which we are considering this factor vies for first place in influencing the benthos with the ever-present stream characteristic, current. Where the bottom is composed of the shifting sands and silts derived from rapidly eroding water sheds little in the way of bottom fauna can maintain a foothold and the benthic communities never approach a condition of stability. Ricker (1934) found, for instance, that in a stream wherein sandy beds constitute most of the bottom he was, "unable to detect any life whatever."

Quite in contrast to this condition is that where swift streams flow over hard bottoms composed of boulders or rock ledges. There a rich fauna is developed and predominant species often occur in tremendous abundance. Again current is of utmost importance, but it is not the water movement itself which is so vital, but instead its secondary effects. Wu (1931) showed that in Simulium larvae this secondary, but powerful, effect of current was not due to the respiratory needs of the animals, as had been previously thought, but to the food-bearing function which it serves. Clingers and burrowing animals dominate the benthic communities of these swift current streams and their very physiological demands which provide the motivating forces in the development of these communities likewise provide those admirable adjustments to the conditions which surround them. Caddis larvae build cases of stone fragments and cement them firmly to the rocks or boulders and construct nets across the current to strain out their food. Mayfly nymphs spread their stream-lined, flattened forms close to the rock surfaces. Turbellarians glide along the lower facets of the stones, and the isopods and amphipods live in the interstices between them.

Every student of stream communities whose work is known to me has agreed that, other things being equal, the sluggish-water stream far surpasses the swift current creeks and rivers in biological productivity. Even within the same stream course where local gradient provides significant differences in fall this fact is borne out, often in a striking manner.

The nekton communities are still composed of the dominant fishes, but the components of the fauna are different. Ricker found that in the warmer, slowly moving rivers of Ontario, "trout do not occur, the important piscivor-

ous fishes being pike and Centrarchids, which are accompanied by a great variety of minnows, suckers, catfish, darters, etc."

The plankton communities are likewise characterized by a much greater richness, diversity and complexity of interrelationship. Eddy found the most mature plankton communities of the streams he studied, "to contain about forty predominant organisms." In such situations stream plankton communities approach, and perhaps even attain, practically the same degree of permanence enjoyed by the lake and pond communities of a similar category.

The bottoms of slowly moving streams are predominantly muddy and sandy. On the rich loam soils of the muddy reaches, aquatic vegetation often attains a luxuriance hardly equaled elsewhere in fresh-waters. And associated with this dense growth of plants a luxuriant fauna of burrowing and phytophagous animals occurs. In such situations, the biotic communities are prolific in both predominants and associates and the interrelationships of the organisms with each other and with their inanimate environment are correspondingly complex.

The long series of publications by Richardson (1921-1928) on the bottom fauna of the Illinois River constitute an important contribution to our knowledge of benthic communities in large streams. These studies dealt in detail with the conditions of existence in situations which were often grossly polluted by both domestic and industrial wastes. This is an aspect of fresh-water biology which although intensely interesting and decidedly important must be here passed with a mere mention of its existence.

Richardson's work also contains some information on another feature of community problems which is a fascinating phase of the subject, namely competitive relations among the bottom animals. As an illustration of this kind of community interrelationship the following excerpt is quoted from his 1928 report. Speaking of the several species of snails which occur in the section of the river where his work was done he says,

> .... the fact that they once became dominant in an area seems to have given them a more or less permanent and, if abundant, often almost undisputed foothold there. This was with little doubt in some part due to the inability of other bottom invertebrates, which plaster minute eggs on solid objects on the bottom, to multiply in great numbers where the rasping tongues of hundreds or thousands of *Campeloma* and *Vivipara* per square yard were in daily operation. The hold of the larger *Gastropoda* on the territory once occupied by them in great numbers was doubtless also strengthened against some otherwise likely associates, by the smothering blanket of slime spread over and binding together the fine bottom ooze and shutting off the air over large areas from eggs or very young stages of other species living therein; and against still others (as possibly *Tubificidae* and young *Chironomidae*) by the sheer bulk, weight, and slow motion of these snails, which could easily result in smothering many small organisms of other sepcies unfortunate enough to be in their way.

In England, more recently, another limnologist has become interested and active in the problem of these competitive relationships of benthic animals. Beauchamp (1932) has worked on such relationships between species of triclads in certain springs, streams and lakes in the lake district of England. He found that in some instances, "*temperature* is the factor which governs the relative success and efficiency of the two species," concerned, while in other

instances the, "governing factor is not so much temperature as the *rate of flow* of the water."

Lentic Communities

Lentic communities, in common with those of the lotic habitats are of two major types, depending upon the place they occupy in the general environment. In all permanent, standing, fresh-waters, biotic associations are capable of being divided into the limnetic and the benthic communities. The open waters of a lake support groups of organisms which fall into three major kinds: neuston, plankton and nekton. The substratum under the waters from shore line to the deepest parts exhibit three well-defined regions, namely the littoral, sublittoral and profundal. Each of these situations offers a wide variety of habitats and the biotic communities vary accordingly.

When circumstances are favorable in the limnetic zone of lakes there occurs a little-studied and somewhat loosely organized assemblage of organisms which are associated with the surface film. One division of the whole group is related to the upper surface of the film, the other to its lower surface. Collectively they are referred to as the neuston. The infraneuston, whose members hang from or float against the lower side of the film draws its components from the bacteria, Protozoa, Algae, Hydra, certain Entomostraca, a few insect larvae and others. Skimming about on the upper surface of the film one may find representatives from several groups of the insects, notably the Gerridae, Veliidae, Hydrometridae, Gyrinidae, and Collembola. These are known as the supraneuston.

One of the most widely accepted and applicable classifications of lakes is that of Whipple (1927), in which these bodies of water are divided into three great groups the polar, temperate, and tropical and further under these three major types into three orders each on a basis of the temperature relations of their limnetic regions. Temperature of the water is one of the most powerful factors which modify the dynamics of lacustrine communities, not so much directly by its own effects as indirectly through its modification of other factors. The sun and the wind combine to produce the phenomenon of thermal stratification and thus set in motion a whole train of causes and effects which are manifest in every community of the lake. Epilimnion, thermocline, and hypolimnion offer exceedingly different habitats for the limnetic organisms.

The great producing class of organisms for the whole lake is the plankton. Other groups within its boundaries contribute to the total production of a lake, but none to such an extent as plankton. Within its own limits it possesses both producers and consumers just as plants and animals exhibit that relationship in the terrestrial realm. But producers and consumers alike are again a source of supply for other great categories of organisms. The green phytoplankters, like their relatives the green plants on shore, utilize both organic and inorganic substances as food and like the higher plants derive their energy for photosynthesis from the sun. In their case, however, food is all about them, dissolved in the ambient medium, ready to be absorbed and utilized in the business of building protoplasm and its products.

Taxonomically fresh-water plankton contains representatives from all but

one class of the Algae, from the bacteria, and the fungi on the plant side while among the zooplankters we may find animals belonging to the Protozoa, Coelenterata, Rotifera, Cladocera, Copepoda, and Ostracoda as the most frequent components with several others straying in as occasional members.

The literature of fresh-water plankton is probably the most voluminous part of all limnological writings. The vast amount of research in the subject has resulted in many systems of classification based on a wide variety of criteria. These systems have been based upon size, upon kind or quality, upon the conditions of their environmental distribution, upon their place and mode of origin, upon differences in their life histories, and on other phenomena. Like all systems of classification each one of these has few or many proponents, as the case may be, and each, no doubt,has served a useful purpose.

Limnetic plankton communities are, in general, governed by the same laws which operate in all organic communities, upon behavior of the constituent organisms, their similar physiological demands, and similarity of habitat. Of Eddy's four types of fresh-water plankton societies referred to before, two belong to lakes and these he describes in the following terms; naming in each instance the predominant organisms and the type of lake in which they abound.

2.—Deep lakes: *Notholca longispina, Striatella fenestrata, Daphnia retrocurva, Bosmina longispina,* and *Diaptomus minutus.*

4.—Moderately deep and shallow glacial lakes: *Diaptomus oregonensis,* pelagic diatoms, and blue-green algae.

Beneath the limnetic region of a lake, forming its floor, lies the second great environmental division of lacustrine habitats, the benthic zone. Probably, fully as many systems of classification of its regions and its biota have grown up and been used to a greater or less degree as have been proposed for the plankton. Moreover, lakes themselves have frequently been classified on the bases of the nature of their bottom deposits and on the character and composition of the benthic biotic communities.

Knowledge of the existence and something of the behavior of the littoral benthic organisms formed a part of the primitive background of limnology. But as a respectably scientific part of the general subject it is still recent. Until less than thirty years ago all benthic studies, except in a few instances which were confined to the upper littoral, were entirely qualitative enumerations of the flora and fauna. Not until 1911 when Ekman introduced the dredge which bears his name did work in this phase of limnology become quantitative. The development of this instrument, however, gave a tremendous impetus to studies of the benthic fauna and today there exists a considerable literature on the subject, whose titles number many hundreds and which has been written in more than fifteen different languages. The principal centers of activity in this work have been in Canada, the United States, the British Isles, Denmark, Germany, Russia, and Japan.

Within the last decade it has become common practice to divide the lake floor into three zones: litoral, sublittoral, and profundal, with minor or secondary subdivisions of these sometimes being recognized. A fourth zone the "abyssal" was proposed by some of the early workers for those great depths,

as fresh-waters go, lying below 600 meters. The suggestion has found little favor and less application, however, perhaps because so little is known concerning benthic biology in the few lakes where it might be expected to exist, notably Baikal, Tanganyika and Crater.

Although the first three benthic zones mentioned above have been almost universally accepted, there is as yet no unanimity of agreement as to their limits nor the criteria on which these limits should be based. In 1931, the speaker proposed a set of limits which have enjoyed some degree of acceptance. They were stated as follows:

> .... the littoral zone of the bottom is.... that region lying between the shoreline and, approximately, the lakeward limit of (rooted) aquatic vegetation. The profundal zone extends from the greatest depth.... up the slope toward shore to a point (it would be better to say isobath) somewhat above that corresponding to the average upper limit of the hypolimnion. The sublittoral lies between these two.

It is obvious that under the terms of these definitions, only those lakes which stratify thermally would have a profundal zone and that in many shallow, clear-water lakes the whole benthic habitat would lie within the littoral. Such is actually the case. No lake should be considered as having a profundal benthic zone unless it stratifies physically or, to some degree stagnates chemically during at least a part of the year. The sublittoral is everywhere a transition zone. Often there lies within its boundaries what Lundbeck (1926) called, "die Schalenzone." The shell zone is well developed in some American lakes, faintly in others, and in still others not at all, even where a source of supply for its construction exists. Around much of the basin of Lake Michigan, for instance, this belt-like burial ground for the dead shells of vast molluscan populations occurs very clearly.

The benthic communities of our lake floors are strongly affected by the physical and chemical nature of the superimposed water. Thermal stratification and the frequently accompanying chemical stagnation sometimes goes so far as to completely wipe out the whole benthic fauna beneath the hypolimnion. The speaker has, for more than ten years, been studying an unusual lake in central New York state where the whole bottom below the 9 or 10 meter isobath is a veritable biological desert. In all the hundreds of bottom samples taken from the profundal zone of that lake not a single living, macroscopic benthic animal has ever been found. Indeed it appears to the speaker that, as stated in his 1931 paper, mentioned before, "Evidence now available indicates that the members of the profundal benthic fauna are facultative rather than obligatory 'anaerobes' and that they endure rather than select an anaerobic environment."

The predominant species of several benthic communities are now known and some knowledge has been gathered concerning their interrelationships. Among those about which most is known may be mentioned the following:

1. The Corethra—*Chironomous plumosus* community, typical of the deeper profundal zone of many north temperate lakes of the second order.
2. The Corethra-Chironomus-Protenthes community, frequently found in the upper profundal and lower sublittoral of the same type of lakes.
3. The Tanytarsus communities of the central European lakes.

Others are recognized but the list need not be continued here.

At least for the sake of completeness, there remains to be mentioned the communities of several other types of the fresh-water environment. Ecologically distinct habitats and equally distinct communities exist in the very many kinds of ponds, bogs, marshes, springs, and in the subterranean waters, both lentic and lotic. Interest in the phenomena of the bog lakes is growing every day among limnologists and many investigations of these intriguing waters are being conducted at the present moment. It has long been known that springs of various sorts harbor scanty but highly characteristic communities. Subterranean waters in caves and elsewhere have been found to possess exceedingly highly selected faunal communities, whose members show many remarkable peculiarities, some well developed, others in the process of evolution.

Present-Day Trends of Fresh-Water Investigations

Partly as a result of the varied interests of its sponsors and partly because of the inherent nature of the subject, fresh-water studies are today following two well-marked aspects of emphasis. One of these is concerned with applied limnology. The regional and watershed surveys, so popular in many states just now, are examples of this phase. Rather sharply in contrast to this work is the research in what might be called basic or fundamental limnology. This aspect of the present trend attracts much less attention, at least in the public press, but naturally is still busy building the foundations on which the former type of work must rest.

Much more fundamental, however, is the cleavage on the point of emphasis into three major phases, which we shall name the environmental, the biotic, and the truly limnological. Environmental studies are extremely important. They are of great assistance to those who follow, but they are often hardly biological. The biotic type of investigation, which was at first strictly qualitative, has within the last two decades become largely quantitative. There are still two phases of these studies. One is extensive, the other intensive.

Prominent among the agencies which foster fresh-water research are the great universities of this country and others. There are at least a dozen universities in Canada and the United States where some one or more investigators are at work, and in a few of these there are several men whose spheres of research lie in limnology. Governmental agencies of various kinds, the established and the new bureaus and commissions of both state and federal governments are actively engaged in forwarding limnological research programs. The many fresh-water biological stations scattered over the earth are all interested, to some degree, in work of this kind.

As indices of progress we may point to the constantly growing volume of publications, both the research literature and formal text-books. The establishment of limnological journals and societies, among them the three-year-old Limnological Society of America, bespeaks a healthy and virile interest in the subject. Still another index of progress is the increasing number of formal courses of instruction now being offered in our universities and colleges.

To return for a moment to the aspects of emphasis which we were discuss-

ing, it has long seemed to the speaker that what we have called the truly limnological is, and must be, a combination of the environmental and the biotic types of work. Our definition of ecology which occurred early in this paper may have appeared a bit redundant because of the word "complete." What was intended was to place emphasis on the fact that any brand of ecology, and that includes limnology, must recognize the existence of the three great realms of environmental influence, the physical, the chemical, and the biological. It is not possible to ignore any one of these and still keep the work truly limnological in character.

Finally, the most recent trend in the subject is the appearance of experimental work in both lake and laboratory. This seems to the speaker to be a most desirable point of emphasis because it is high time the subject ceased to be purely observational and began to seek causes. But as we work let us remember that we are studying living organisms, not merely their habitat or environment and let us further remind ourselves constantly of the unity of the forces which play upon these organic beings. Factors vary in intensity and effectiveness, but they always vary in *the presence of all the other factors of the environment*. No one factor, ever operates alone. The biotic community is within the grip of almost unbelievably complex interrelationships but those interrelationships are not chaotic. They are logical and law-abiding. Therein lies the hope of puny man, in his daring attempt to understand them.

REFERENCES

ADAMSTONE, F. B. 1924—The Distribution and Economic Importance of the Bottom Fauna of Lake Nipigon with an Appendix on the Bottom Fauna of Lake Ontario. Univ. Toronto Studies, Biol. Ser., Pub. Ont. Fish. Res. Lab. **24**:35-100.

———AND W. J. K. HARKNESS. 1923—The Bottom Organisms of Lake Nipigon. Univ. Toronto Studies, Biol. Ser., Pub. Ont. Fish. Res. Lab. **15**:123-170.

BAKER, FRANK C. 1916—The Relation of Mollusks to Fish in Oneida Lake. N. Y. State Coll. Forestry, Tech. Pub. No. **4**:1-366.

BEAUCHAMP, R. S. A. AND P. ULLYOTT. 1932—Competitive relationships between certain species of fresh-water triclads. Jour. Ecol. **20**(1):200-208.

BIRGE, E. A. 1904—The thermocline and its biological significance. Trans. Am. Micro. Soc. **25**:5-33.

———AND C. JUDAY. 1922—The inland lakes of Wisconsin. The plankton. I. Its quantity and chemical composition. Wis. Geol. Nat. Hist. Surv., Bull. **64**, Sci. Ser., **13**:1-222.

CARPENTER, KATHLEEN E. 1928—Life in Inland Waters with Especial Reference to Animals. Macmillan Co., N. Y. xviii + 267 pp.

CHANDLER, DAVID C. 1937—Fate of typical lake plankton in streams. Ecol. Monogr. **7**(4):445-479.

EDDY, SAMUEL. 1934—A Study of Fresh-water Plankton Communities. Ill. Biol. Monogr. **12**(4):1-93.

EGGLETON, FRANK E. 1931—A limnological study of the profundal bottom fauna of certain fresh-water lakes. Ecol. Monogr. **1**:231-332.

EKMAN, S. 1911—Neue Apparate zur qualitativen und quantitativen Erforschung der Bodenfauna der Seen. Int. Rev. Hydrobiol. **3**:553-561.

JUDAY, C. 1921—Observations on the larvae of *Corethra punctipennis* Say. Biol. Bull. **40**(5):271-286.

———1922—Quantitative studies of the bottom fauna in the deeper waters of Lake Mendota. Wis. Geol. Nat. Hist. Surv. Bull. **15**:461-493.

KOFOID, C. A. 1903—The Plankton of the Illinois River, 1894-1899, with Introductory Notes upon the Hydrography of the Illinois River and Its Basin. Part I. Quantitative Investigations and General Results. Bull. Ill. State Lab. Nat. Hist. **6**:95-629.

KUSTER, KIMBER C. 1934—A Study of the General Biology, Morphology of the Respiratory System, and Respiration of Certain Aquatic Stratiomyia and Odontomyia Larvae (Diptera). Papers Mich. Acad. Sci., Arts and Let. **19**:605-658.

LUNDBECK, J. 1926—Die Bodentierwelt norddeutscher Seen. Arch. f. Hydrobiol., Suppl. **7**:1-473.

MARSH, C. D. 1899—The Plankton of Fresh Water Lakes. Trans. Wis. Acad. Sci., Arts, and Let. **13**:163-187.

MIYADI, D. 1931-1933—Studies on the Bottom Fauna of Japanese Lakes:
1931a—I. Lakes of the Sinano Province. Jap. Journ. Zool. **3**:201-258.
1931b—II. Mountain Lakes of the Tributaries of the River Tone, with Special Reference to the Azoic Zone. Ibid. **3**:259-298.
1932—III. Lakes of the Kwanto Plain. Ibid. **4**:1-40.
1932—IV. Lakes of the Japan Sea Coast of Southern Honsyu. Ibid. **4**:41-80.
1932—V. Five Lakes at the North Foot of Mt. Hudi and Lake Asi. Ibid. **4**:81-126.
1932—VI. Lakes of Southern Kyusyu. Ibid. **4**:127-150.
1932—VII. Lakes of Kokkaido. Ibid. **4**:223-252.
1932—VIII. Lakes of North Japan. Ibid. **4**:253-288.
1932—IX. Lakes of the Yodogawa-basin. Ibid. **4**:289-314.
1933—X. Regional Characteristics and a System of Japanese Lakes Based on the Bottom Fauna. Ibid. **4**:417-438.
1933—XI. Lakes of Etorohu-Sima Surveyed at the Expense of the Keomei-Kwai Fund. Ibid. **5**:171-208.

MUTTKOWSKI, R. A. 1918—The Fauna of Lake Mendota: A Qualitative and Quantitative Survey with Special Reference to the Insects. Trans. Wis. Acad. Sci., Arts and Let. **19**(1):374-482.

NEEDHAM, J. G. AND J. T. LLOYD. 1930—The Life of Inland Waters. 2d ed. Springfield, 438 pp.

PEARSE, A. S. 1926—Animal Ecology. New York, 417 pp.

RAWSON, D. S. 1930—The Bottom Fauna of Lake Simcoe and Its Role in the Ecology of the Lake. Univ. Toronto Stud., Publ. Ont. Fish. Res. Lab., **40**:1-183.

REIGHARD, J. E. 1894—Some Plankton Studies in the Great Lakes. Bull. U. S. Fish Comm. for 1893, pp. 127-142.

RICHARDSON, R. E. 1921—The Small Bottom and Shore Fauna of the Middle and Lower Illinois River and Its Connecting Lakes, Chillicothe to Grafton: Its Valuation, Its Sources of Food Supply, and Its Relation to the Fishery. Ill. State Nat. Hist. Surv. Bull. **13**(15):363-521.

———1925—Changes in the Small Bottom Fauna of Peoria Lake, 1920-1922. Ibid. **15**(5):391-422.

———1928—The Bottom Fauna of the Middle Illinois River, 1913-1925: Its Distribution, Abundance, Valuation, and Index Value in the Study of Stream Pollution. Ibid. **17**(12):387-475.

RICKER, WILLIAM E. 1934—An ecological classification of certain Ontario streams. Univ. Toronto Stud., Biol. Ser. No. **37**; Pub. Ontario Fish. Res. Lab. **49**:1-114.

SHELFORD, VICTOR E. 1918—Conditions of Existence. Chapt. II in Fresh-Water Biology. Wiley, N. Y. pp. 21-60.

———1913—Animal Communities in Temperate America. Chicago, 362 pp.

VAN DER SCHALIE, HENRY. 1938—The Naiad fauna of the Huron River, in southeastern Michigan. Univ. Mich., Museum of Zoology, Misc. Pub. No. **40**:1-83.

WELCH, PAUL S. 1935—Limnology. New York. xiv + 471 pp.

WESENBERG-LUND, C. 1908—Plankton Investigations of the Danish Lakes. Copenhagen. 389 pp.

WHIPPLE, G. C. 1927—The Microscopy of Drinking Water, 4th ed., rev. by Fair and Whipple. New York, 586 pp.

WIEBE, A. H. 1928—Biological Survey of the Upper Mississippi River with Special Reference to Pollution. Bull. U. S. Bur. Fish. **43**:137-167.

WU, YI FANG. 1931—A Contribution to the Biology of Simulium (Diptera). Pap. Mich. Acad. Sci., Arts and Let. **13**:543-599.

DISCUSSION

Park: I would like to get a little more detailed distinction between truly limnological, environmental, and biotic factors.

Eggleton: This classification distinguishes three fairly well marked aspects of limnology: 1) the study and interpretation of physical and chemical factors of the environment; 2) the qualitative and quantitative determination of the organisms of a specific area, a unit area, or a whole region; and 3) the truly limnological, a combination of these two, i.e. the truly ecological approach.

Conard: Might I suggest the term *limno-sociological* for a truly limnological study?

Mottley: What is biological productivity and how is it measured?

Eggleton: According to Welch, "biological productivity" means simply this: the kinds and quantity of organisms which may be produced under a given set of environmental conditions. We may think of biological productivity in terms of commercially and economically important organisms, but it is also possible to think of biological productivity in terms of the commercially least important organisms, as for instance, plankton. We think of biological productivity in terms of the amount of life, of whatever kind, which a given body of water is capable of producing under a given set of conditions. There are various ways of expressing biological productivity but I do not know of any one term which will express the whole thing. I suppose it is a reflection of the finite nature of the human mind that we should choose to represent it in terms of numerical abundance of organisms of any particular kind at any particular time. Perhaps that does not express the whole idea of biological productivity and I know I would be grateful for a suggestion to express it in a better way.

MacGinitie: How many plankton communities are found in Fayetteville Green Lake, and how are they separated?

Eggleton: Nearly all the research I have done in this lake pertained to benthic organisms. I do not know what the plankton communities of this lake are. It seems, however, that benthic organisms can be more readily referred to benthic communities than plankters can to plankton communities. For instance the *Corethra - Chironomus*

plumosus community is typical of the deeper profundal zone of many of our temperate lakes of the second order. If large enough samples are taken over a series of months or preferably over a series of years, because there is a very marked seasonal fluctuation, an assemblage of organisms will be obtained which is composed almost entirely of *Corethra*, *Chironomus*, and *Protenthes* larvae, one or two species of the Tubificidae, and sometimes one species of *Pisidium*. Those are practically all the organisms occurring in that assemblage. *Corethra* might be selected as the dominant organism of the association or community and that particular group of organisms might be called a community. This use of the term, however, migh not agree with the way plant ecologists and oceanographers use it.

Mottley: How can one community be made up in one way during one part of the day and another way during another part of the day? It ceases to be a single benthic community since the *Corethra* move into the surface water at night.

Eggleton: *Corethra* larvae are typical of this benthic group and they are there in some phase of their life history at all times, day and night. Not all of these larvae migrate to the surface at night, instead many remain in the bottom mud. Moreover not all the life history stages migrate to he surface.

Mottley: If they are moving from day to day it will be rather difficult to work out population curves. How many samples should be taken?

Eggleton: It is necessary to take many samples because of seasonal fluctuations. In a little just outside Ann Arbor I have collected a great many samples. In midwinter these profundal benthic organisms sometimes reach the tremendous number of 71,000 per sq. meter. They are not the only organisms there, but they dominate the community numerically and incidentally migrate considerably up to the surface in midwinter.

Mottley: What type of distribution is found?

Eggleton: There is often a very uneven distribution over small areas.

Mottley: Organisms may be distributed in nature in such a way that we have no method of dealing with the data. We can draw curves, but we have no way of predicting what the samples will tell us of the living world.

Just: Another noteworthy trend of limnology is Naumann's "regional limnology" with its geological basis.

Eggleton: Naumann, in his classification of limnology, has given us a large number of useful ideas.

The Biome

J. Richard Carpenter

In presenting the concept of the biome it will perhaps be best first to state the principles of the concept, then to trace the development of its component ideas, and finally to analyze its significance. The concept of the biome is dual, i.e., first, biotic communities exist in nature, and second, the biome is the primary unit of bioecology possessing formational rank (*sensu* Clements). The views of some of the European bioecologists will be considered later, but since most of the proponents of the biome are Americans, we will begin with a brief account of the development of their ideas.

The following quotation will give a concise statement of the concept.

> The primary unit of bioecology is the biome, a community of formational rank in the largest sense of the term. The biome is characterized by uniformity of physiognomy of the plant climaxes and in a lesser way by the climax stages. It is characterized by a combination of major and minor influent animals, a few climax influents, and many small influents and subinfluents. A certain grouping of species and varieties is characteristic of each biome. The biome or bioecological formation is based upon both plants and animals. Bioecology considers that plants and animals are inseparably united in the structure of any community. (Shelford & Olson, 1935)

As Phillips (1931) and Taylor (1935) pointed out, there are three essential ways of considering the relations between plants and animals: (1) that animals are biotic factors independent of the plant community; (2) that there are animal communities to which plants are a portion of the habitat; and (3) that plants and animals are constituents of an integrated biotic community. A fourth viewpoint was suggested by Allee (1934, p. 552) and Tansley (1935): if animals are included in the concept of the community, the habitat should be included as well. This is also Elton's idea, as expressed in the term "ecosystem," and is comparable to the "coen" of Heck and the "holocoen" of Friedrichs (1930, p. 233).

The first viewpoint, that animals are but biotic factors or features in the plant community, can be readily dismissed since it offers little towards the formulation of a biotic concept. Unfortunately this view is taken by many plant ecologists, although they frequently recognize that "animal life has a powerful influence upon the kind and the economy of vegetation" and that "between the plant life and the animal life there exists an intimate and complex reciprocal relation".* Such statements may be considered to pertain to the recognition of another environmental factor, much as some animal ecologists consider plants to be a portion of the animal's habitat. The second viewpoint is of historical interest showing as it does the development of ideas which culminated in the third viewpoint, the biotic concept. A chronological

* Warming, 1909, pp. 82 and 77 respectively; Phillips (1931, p. 3), however, is inclined "to doubt whether Warming was a staunch supporter of the view that animals act as factors external to the plant community."

presentation of the views may reveal several seeming anachronisms since one may read into earlier papers what one wishes to find.

One of the earlier studies on animal communities was that of E. Forbes (1844) on the Mollusca and the Radiata of the Ægean. He recognized certain "provinces of depth" and listed certain species as characteristic of, but not necessarily limited to, each zone, being perhaps more abundant there than elsewhere (see Allee, 1934, p. 542).

Another early study is that by Verrill & Smith on the invertebrates of Vineyard Sound (1871). "In prosecuting our explorations we soon find that there are, in the waters of this region, three quite distinct assemblages of animals and animal life which are dependent upon and limited by definite physical conditions of the waters which they inhabit." These groupings, similar to those used much later by Dahl and by Pearse, were the fauna of (1) bays and sounds, (2) of estuaries and other brackish waters, and (3) of ocean shores, outer banks and channels.

Apparently Möbius (1877)* was the first to consider an aggregation of animals a community (p. 722). "Every oyster bed is.... a community of living beings, a collection of species, and a massing of individuals, which find everything necessary for their growth and continuance.... Science possesses, as yet, no word by which such a community of living beings may be designated; no word for a community where the sum of species and individuals, being mutually limited and selected under the external conditions of life have.... continued in possession of a certain definite territory. I propose the word Biocönosis for such a community." Although no direct mention was made of the habitat restrictions of the community, Möbius did point out the environmental features "necessary for the growth and continuance," i.e., "suitable soil, sufficient food, the requisite percentage of salt and a temperature favorable for their development." He also contended that "each species is represented by the largest number of individuals which can grow to maturity subject to the conditions which surround them," intimating the existence of a "biotic capacity", as yet but poorly understood.

The third of the earlier studies, also on aquatic communities, that of Davenport (1903) on the animal ecology of the Cold Spring Harbor sandspit, uses the habitat or zone, rather than the actual distribution of the organisms, as the unit of study, but emphasizes the interrelations of organisms within each habitat. A comparison was made between the animal communities found on the Cold Spring Harbor sandspit and those on the Jackson Park Beach at Chicago, and the author notes that the general ecological structure of both areas is similar. "The fauna is determined by definite proximate causes of a simple sort [("not too complex to be unraveled")] that act, the world over, in the same way, and so give to a similar sea beach in other parts of the world a similar collection of animals—excepting that each species may be replaced by another" (p. 171).

* Original in German; citations here taken from the English translation of 1880, U. S. Fish. Comm., part 8, pp. 721-729.

The realization that similar areas in different districts have similar inhabitants was also brought out by S. A. Forbes (1907, p. 273-4) in discussing the dynamic interrelations within a community:

> An animal society is composed of animals habitually occurring together in the same locality and the same class of situations. Such an association is composed of many species variously related to their special environment, some attracted to it by one set of conditions and some by another.... For a full study of the intricate web of relations to their physical environment, and through that to each other, it is necessary that the entire assemblage of the inhabitants of that area should be studied as a compound unit.

Whether or not plants should be included is not stated specifically.

In the *Ecological Survey of Isle Royale, Michigan* (1908) statements by Adams and Gleason show a marked trend towards the biotic idea. Much of the report dealt with the communities found, and with the determination of their successional and developmental relationships. Since both plant and animal ecologists were working together and collaborating—the ideal situation—local plant and animal distributions assumed a significant relationship. Gleason uses the term "climax biotic association" (p. 57) several times and states (p. 58) that "a biotic association may develop into another by a rearrangement of the interrelations, numerical or otherwise, of the component species." Adams likewise remarks (p. 148) that "the climax society is in a state of biotic and environmental equilibrium," and again (p. 143-4) that "the dominant biotic tendency or dynamic trend.... is for the conifer biotic areas to encroach upon all other societies and habitats and to become the dominant or universally distributed association or formation." However, in another portion of the report, Adams says (p. 134): "by an avian formation, or society, is meant different combinations of species which regularly occur together in the same breeding habitat or area" and (p. 131) "an avian formation may, in general terms, be considered the analogue of a vegetational formation, although this does not imply that they necessarily have the same boundaries." Consequently at that time Adams considered animal and plant communities to be distinct, although closely related—analogues was his term.

In Shelford's early tigerbeetle work (1907, 1911) the vegetation is considered as a portion of the habitat of the animal (1911, p. 601): "The vegetation from the standpoint of whether it is forest, steppe, or desert, etc., does not involve animals.... [(but)] .... it is the most important factor in the control of temperature, moisture, light, food and materials for abode and is a good index of the conditions which surround animals. Tentatively it may be used as a basis of classification of animal environments." In the following year a paper entitled *"Vegetation and the Control of land Animal Communities"* (1912, p. 93, § 6) contains the statement that "plant and animal communities are divisible into the strata which represent vertical differences in physical conditions." In his book *Animal Communities in Temperate America* (1913, p. 307; also 1915, p. 20), the animal communities are characterized by the plant communities of the area. "Plant and animal communities may be said to be in full agreement [(physiologically)] when the growth form of the plant community is correlated with the conditions selected by the animals of that

stratum." This physiological viewpoint led to the discovery of the principle of the "mores" of a community which will not be treated here.

The Danish school of marine biologists had meanwhile been developing concepts regarding sea bottom communities, which will be taken up here, rather than with the other European viewpoints, because of the influence on and the comparative agreement with the American concepts. In 1911 Petersen and Jensen pointed out that certain species could be considered as "predominants" and characterized their communities by the organisms and their distribution, not by the physiographic habitat.

> The animals, which are not seasonal and which compose an important part of the whole mass of the community, owing to number or weight, will presumably be best for characterizing the community and must also be considered as giving a good idea of the outer conditions on which the community is dependent. (Petersen, 1913, p. 4-5).

> I am of the opinion, therefore, that as a rule it is best to regard the animals living on the seabottom as communities, just as botanists group together the vegetation of the land into plant communities. (*Ibid.*, p. 32).

Since these were marine bottom communities, the question of including plants did not arise.

I will mention only in passing the studies of Hart & Gleason (1910), Baker (1910), and Adams (1915), since they did not contribute materially towards the further development of this concept. On the other hand Vestal (1913, 1914) was much more inclined towards the biotic concept of the community and it is here that the earliest definite statement regarding it is made.

> The internal activities of the association may be said to be the sum total of the activities of all the plants and all the animals which make up the association (1914, p. 414). In terrestrial climatic or extensive environments, the relations between the assemblage of plants and the assemblage of animals are intimate and regular of occurrence, so much so that (1) the two are coextensive, (2) the two constitute what may be called a biotic association, (3) neither plant nor animal assemblage usually occurs independently of the other [p. 429-30]. In ordinary climatic development of plant and animal life in temperate land environments, the area of the animal assemblage is that of the plant assemblage, both resting basically upon the physical environment. The plant and animal assemblages are therefore coextensive parts of a biotic association composed of both plants and animals, and this association as a whole constitutes a real terrestrial community of living organisms [p. 435]. Plant and animal assemblages are essentially interdependent . . . . , correspond in geographic distribution into communities, and in more detailed distribution with the habitats [p. 444].

In 1916 Clements proposed the term "Biome" for a biotic community consisting of both plants and animals. The abstract of his paper as printed in the program of the New York meeting of the Ecological Society of America reads as follows:

> The biotic community is regarded as an organic unit comprising all the species of plants and animals at home in a particular habitat. While plants are regarded as exerting the dominant influence in the community, it is recognized that this rôle may sometimes be taken by the animals. The biotic community, or biome, is fundamentally controlled by the habitat, and exhibits a corresponding development and structure. In its development the biotic formation reacts upon the habitat, and thus produces a succession of biomes, comparable in practically all essentials to the succession of plant communities.

It is noteworthy that the term is here used as synonymous with "biotic community" and not in its present sense which has reference to the biotic formation.

It seems of little value to trace further the development of the idea that plants and animals constitute biotic communities. This fact is now fairly generally accepted by those who have studied simultaneously both elements of the biota, although others without this experience are still dubious. The recent literature on the biotic community may be found in the extensive bibliographies of Phillips (1931), Taylor (1935), Shelford *et al.* (1935), and Carpenter (1936, 1937); additional papers worthy of particular notice are those of Woodbury (1933), Swynnerton (1936), Beed (1936), Williams (1936), Hefley (1937), and Shelford *et al.* (1935).

Acknowledging the fact that both plants and animals form biotic communities, a basis must be established upon which community units may be graded. As shown previously, the element of succession played an important part in the development of the concept of the dynamic biotic community; this is certainly true for England and America. It is not surprising, therefore, that workers in bioecology have selected as their unit the climax formation (*sensu* Clements). As will be recognized immediately, the biome has essentially the same units which have been proposed for the *plant formation* of Clements. It is the purpose of this paper to review not those principles of the Clementsian system which are well known, but rather the less well known features relating more particularly to the newer biotic concepts and the innovations necessitated by the addition of the animal components. The following catalog of terms and their definitions will serve as an outline of this system.

I. "The largest natural unit is the *Biome* or *Biotic Formation*" (Shelford, 1932, p. 110). The fundamental units are the largest, i.e., those of formational rank (Anglo-American sense, equal to the "vegetational region" of Du Rietz, 1929). The formation in this sense is of the magnitude of the deciduous forest, the prairies, the northern transcontinental coniferous forests, etc. This is "the climactic climax of succession which terminates in the highest life forms possible with the available biota in the climate concerned" (Woodbury 1933, p. 168). "Its character is revealed by the dominants or controlling species of which it consists; all these belong to the same [(growth)] form" (Weaver & Clements, 1929, p. 44). "The biotic formation includes all the developmental stages. This is necessitated by the habits of the large influential animals (mammals and birds) which range over the climaxes and subclimax stages" (Shelford, 1931, p. 456).

II. The unit composing the biotic formation or biome is the biotic *Association*, which is a "biotic unit, characterized by its essential homogeneity of structure (at least with regard to its dominant groups), biotic composition, and physiognomy, usually involving more than one dominant, but including the entire population of a given habitat" (Woodbury, 1933, p. 168). An association includes all developmental as well as climax stages.

III. Within the associations occur communities of lesser rank, each dependent upon the nature of its dominants, its stability in succession and

development, and its habitat. These subsidiary units based upon the variation of the biota (as distinguished from the successional stability of the community) are:

a. The *Faciation* which is a portion of an association in which one or more dominants have dropped out for reasons of variations in local climate, etc., and have possibly been replaced by other forms, yet the general aspect, structure, and physiognomy of the community remain unchanged;

b. The *Consociation* which is a local variant of an association controlled by a single dominant, the others having dropped out because of local conditions and/or competition;

c. The *Presociation* which is a local variant of an association characterized by the marked presence or absence of one or more predominants (animals on land). Although this unit is characterized by animals on land, it should be used with understanding that it is *not* the "animal community" of earlier papers, but merely a unit within the biotic association as well as an integral part of it. When first introduced and used in its developmental form (presocies) (Smith, 1928; Shackleford, 1929) this fact was not well brought out;

d. The *Society* which is, in the usual sense, a subordinate community, characterized by one or more subdominants (plants on land); *seasonal, local,* and *stratal* or *layer* societies have been recognized. The old seasonal society is now termed the *Sociation;* the stratal or layer society is called a *Lamiation* and its seasonal variants are designated the *Sation* (Clements, 1936, pp. 276 ff.). Woodbury also recognizes a *Subsociation* (roughly equivalent to the old local society of Clements) defined as "a morphological part of an association characterized by the conspicuous presence of one or more subdominants under the general influence of the dominants";

e. The *Lociation* which is a local variant of an association, varying in the composition of the more important subdominants and influents, the dominants remaining the same.

IV. As noted above, both the formation and the association include within their boundaries developmental communities of less than climax rank. *Associes* is the term applied to all communities which are not of climax rank and stability. Although various definitions have been given to this term (as well as to the other terms under consideration: see *An Ecological Glossary,* Carpenter, 1938) it may be said to be a developmental biotic community and hence the successional unit, i.e., it has all the attributes of an association save that of stability in development. Like the association it possesses a homogeneity of structure, biotic composition, and physiognomy, usually has more than one dominant, and consists of the entire biotic population of the area involved. All of the associes within the area of a biotic formation, i.e., all of the developmental stages within a given biome, considered collectively, constitute the *Formies.* Units within the associes correspond to those within an association, the *Facies,* the *Consocies,* the *Presocies,* the *Socies,* the *Lamies,* the *Saties,* and the *Subsocies.* The comparative chart given in Table 1 gives a comparison of the relative rank of these communities and the basis of their distinction.

TABLE 1

The Subdivisions of the Biome.

Character	Climax Units	(Plants)* Dominants	(Plants)* Sub-dominants	(Animals)* Predominants, Major Influents	(Animals)* Subinfluents, Minor Influents	Subclimax Seral Units
Per-annual	Association[1]	a, b, c		x		Associes[1] Pre-associes[2]
	Presociation			x		Pre-associes complexes[2]
	Faciation[1]	a, b, c + d a, b — c				Facies[1]
	Consociation[1]	a				Consocies[1]
	Lociation	x	x			Locies
	Subsociation		x			Subsocies
	Lamiation		x			Lamies
Seasonal	Sation		x		x	Saties
	Sociation[3]		x		x	Socies[3]
	Presociety[3]				x	Presocies[3]
Intra-diel	Phase[4]			x	x	Phase[4]

1 Distribution of dominant species (plants on land) (a, b, and c) may result in one dominant (c) dropping out, thus causing a Faciation (composed of a and b), or all save one may drop out, leaving a "pure stand," or Consociation (of a). A Faciation may also be formed by the addition of another dominant (d) thus forming a Faciation of a, b, c + d).

2 Only rarely will predominants be restricted to a single seral stage; hence the designations of Pioneer (or Initial), Midseral, and Subclimax Pre-associes-complexes of seral stages may be applied.

3 Classed as Prevernal, Vernal, Estival, Serotinal, Autumnal, and Hiemal or Hibernal.

4 Classed as Auroral, Diurnal, Vesperal, and Nocturnal phases.

* Plants are usually considered as the dominants on land and animals in marine and deep freshwater communities.

In examining the importance of these principles emphasis will be placed primarily upon their biotic and zoölogical aspects, since their botanical significance has been sufficiently elaborated in the papers of Clements and others.

The biome is a biotic formation, and as such is of the size of the greater biotic zones found on all continents. These biomes are primarily determined by climate, and only secondarily by edaphic factors of the habitat. Recent investigations on climate (e.g., Thornthwaite, 1931, 1933) reveal a close correspondance between climatic areas based on the seasonal distribution of rainfall and temperature and the areas of the biotic formations. The characteristics and biota of several biomes have been studied in detail (Shelford & Olson, 1935, Carpenter, 1939). Shelford & Olson state, in defining the

extent of the coniferous forest biome, "the plant climax is accepted as the guiding principle in the evaluation of the subclimax stages and as delimiting the biome" (p. 396). "The biome is characterized by the uniformity of physiognomy of the plant climaxes and in a lesser way by the sub climax stages. It is characterized by a combination of major and minor permeant influent animals, a few climax influents, and many small influents and subinfluents. A certain grouping of species and varieties is characteristic of each biome" (p. 399).

Within a biome, such as the North American grasslands, having a great north-south extension, many forms do not occur throughout its area, although some species may do so. The essential ecological structure remains the same, even though many forms are replaced in various latitudes by ecologically equivalent varieties or species. The following discussion of the North American grasslands biome is based on the author's own study (Carpenter, 1939).

Within the grasslands biome or biotic formation three biotic associations are recognizable: the "tall grass prairie," the "short grass plains," and the "mixed grass prairie," and, although in some respects the latter may be considered an ecotone, inasmuch as it is a "meeting place for two floras," its broad extent seems to warrant associational rank. The mixed grass prairie is bounded to the west by the short grass plains, on the east by tall grass prairie. The eastern border of the latter is a more distinct ecotone, the transition to the deciduous forest. The prairies of Minnesota, eastern Iowa, and northeastern Missouri are of the same general character as those of Illinois: relict patches of perhaps former climatic climax prairie intermingled with encroaching forest. Since their ecological biota is essentially similar to that of the climax prairies, it must be recognized that a given biotic community can be present in more than one biotic formation, varying its position regarding the climax. Another example of this furnished by the successional stages of the grasslands is presented below. The biotic associations of the grasslands are as follows:

The *Andropogon-Bouteloua-Bison-Canis* (Grasslands) BIOME

Bouteloua-Bulbilis-Bison-Antilocapra (short grass plains) ASSOCIATION
Andropogon-Bouteloua-Bison-Antilocapra (mixed grass prairie) ASSOCIATION
Andropogon-Bison-Canis (tall grass prairie) ASSOCIATION
[*Andropogon-Silphium-Citellus* (postclimax "Illinois" prairie) ASSOCIES]

In mapping the prairie areas from which the dominant plants have been reported as such a central area similar to the "centers of plant distribution" will result. This center for the prairie lies in Nebraska. The "ranges of dominance" of various species extend to the north, south and east, the species more characteristically northern dropping out in the south, and so on. In other words, the tall grass prairie possess three types which vary slightly from the "typical" prairie: an eastern, postclimax relict, a northern faciation, and a southern faciation. Since the animal components of this association vary as to abundance and influence much as the plant dominants, the *presociations* and the *faciations* have here the same distribution.

Pure stands of a single dominant may frequently be found in local areas within the prairie: *Andropogon furcatus, Spartina michauxiana, Stipa spartea,*

and *Sporobolus* frequently form these *consociations*. Local areas conspicuous by the presence of non-grasses are frequent; these are the *subsociations* of Woodbury or the *local societies* of Clements. Layering, the forming of strata or *lamiations*, is common: Weaver & Fitzpatrick (1934, p. 125) find and illustrate clearly as many as 4 lamiations in a prairie in Nebraska (1. *Fragaria-Viola-Galium;* 2. *Steironema;* 3. *Andropogon furcatus-Sorghastrum;* 4. *Elymus-Spartina-Asclepias).* The insects show very characteristic lamiations which change within the periods of each day. The seasonal changes and the formation of *sations* within each layer are well known.

In general, the developmental seral stages belonging to the biome lead to the climax of the association of the region. Few detailed successional studies on grasslands are available, but that of the ravines in Oklahoma may be used as an example (Carpenter, 1937). Here the final stage of succession initiated by erosion is prairie unless gulleying has progressed too far, whereupon the sere is diverted to the edaphic climax of the floodplain forest of the region (Hefley, 1937). Certain stages of Hefley's sere correspond closely to those of George-Barclay (1924) in the upper Mississippi river forest near Minneapolis. This fact supports the contention that seral communities (i.e., those of associes rank) in widely separated areas exhibit sufficient similarity firstly to be considered together belonging to the same *formies,* and secondly, being edaphic and hence distributed less dependently on the climatic regions, they tend to develop into the climax of the particular region concerned.

This is probably not the place to enter into an extended discussion of the internal operations and interactions, coactions, and reactions which take place within a biotic community. Nevertheless, the essential features of the biome concept are based upon these interrelations and are probably among the more striking principles of modern ecology. It seems trite to exemplify these interactions by the rather obvious effects of animals upon vegetation through feeding, trampling, and their part in the nitrogen cycle. Less conspicuous is the effect of the number of smaller animals on an area of ground which has been affected by large herbivores; examples are the greatly increased number of grasshoppers in the Wichita Mountains Wild Life Refuge in Oklahoma and of jackrabbits on the Arizona plains.

Elton introduced the concept of the ecological "niche" as a part of the general ecological structure of the community, each niche being occupied (or not) by organisms "doing" the same things in the community, i.e., being, in a sense, ecologically equivalent. He pointed out that the animals occupying niches differ in number and size, and that the largest number of animals is that feeding directly upon the vegetation, while a smaller number feeds upon these phytophagous forms, a third group feeds upon the second, and so on. Each of these successive groups is composed, in general, of fewer and, frequently, larger forms. This he calls the "pyramid of numbers," an essential feature in many communities: a decreasing number of forms in the niches further removed from direct dependence upon the plants for food. Additional studies are needed regarding the exact constituents of and the activity within these niches, the actual effect of large numbers of small forms upon the community, and the significance of the total "biomass" of any biotic community.

As mentioned previously, Möbius originated the term "Biocönosis" in 1877. Ten years earlier, however, von Post had pointed out the importance of "statistics of organic nature" in studies which he termed "animal and plant topography" and his recommendations on recording animal and plant numbers are admirable. Another pre-Möbius worker was G. Jäger who published an account of the land animals of Germany according to their habitat (Standort). Möbius gives a list of the habitats or environments (Lebensbedingungen): the beach, the regions of the live and dead sea grasses, of the red algae, etc. This method of designating the area of communities was followed by Dahl who gives (1903) a long list of habitats (Biotops) somewhat similar to Pearse's system (1926). No statement can be found in these earlier papers regarding the inclusion of both plants and animals in the concept of the biocenosis.

Palmèn (1908) uses a similar topographical viewpoint. Gams (1918) offered a joint animal-plant system of classification of habitats based on the synusium, but it has been rejected by many European animal ecologists (e.g., Friedrichs, 1930, p. 33-34; Palmgren, 1927, p. 7). This topographic basis for the recognition of communities has been used since, and Friedrichs expresses surprise at the comment of Jones (1926) that it is necessary to determine the community on the basis of the distribution of the organisms themselves rather than on the basis of the distribution of the habitats (Friedrichs, 1930, p. 60). Here lies one of the fundamental differences of opinion between American and continental European bioecologists. Friedrichs defines the community as follows: "The whole animal and plant population of a biotop is its biotic community *(Lebensgemeinschaft)* or biocenosis."

Certain Scandinavian and Russian workers gradually abandon the topographic criterion. The views of the ecologists of the Danish Marine Biological Station have been mentioned. Palmèn (1927) recommends the adoption of Cajander's "forest types." Minin (1936) recommends using the term habitat for the whole complex of ecological conditions necessary for the complete life cycle of the populations, and Veitzman (1936) suggests certain refinements of this interpretation. Until recently Russian ecologists considered the animal communities as independent of the plant communities, recognizing, however, that certain types of the former are restricted to certain types of the latter, but not that the two components belonged together in the biotic community. Since about 1930 they, too, inclined towards a biotic community concept as evidenced by Kashkarov's two textbooks (1933, 1938). In a recent personal communication Kashkarov says: "Both plants and animals belong to the biocenosis (the biotic community of the American ecologists) and such things as 'phytocenoses', 'zoocenoses', 'ornithocenoses' and so on, do not exist in nature." * This is significant in light of the large amount of

* A similar idea is expressed by Allee (1927): "There are no insect communities in nature. They exist only as an abstraction. Rarely, for that matter, are there plant or animal communities. Really, there are only biotic communities, i.e., groups of plants and animals which are more or less closely integrated into a community system."

ecological work in the USSR at the present time, although many of the Russian geobotanists still cling to the phytocenosis as their unit.

Apparently no extensive studies considering both plants and animals have been made using the biocenosis or the phytocenosis as the unit. The use of the latter in the analysis of the sociological distribution of plants is recognized, but the practicability of its application in the biotic sense remains to be demonstrated. Certain Scandinavian and German studies, as well as earlier Russian studies (e.g., Bei-Bienko) used the biotop (habitat) as the unit, but, as was mentioned, failed to consider both plants and animals. Moreover, the proponents of the "biotop" lack higher units to cover areas occupied by a biome.

The large units forming the subdivisions of the biome conform to the behavior of both plants and animals (and are the only ones agreeing with such wide ranging animals as the larger predominants and influents), whereas the smaller units of the phytosociologist or geobotanist are incapable of doing justice to the distribution patterns of these larger forms. Whether or not the distribution of such smaller animals as insects, spiders, snails, etc., conforms to these latter units is still a problem. The more detailed sociological relationships of plants may differ from those of animals, requiring small plant and animal units, but these sociological units make up communities composed of both plants and animals. It is imperative, therefore, that the fundamental unit in any ecological classification should be one in accordance with the phenomena displayed by all components of the community, whether it be forest, grassland, or sea. The only unit apparently fitting these requirements is the biome.

The passages and authors cited above show that the practicability and even the possibility of including both plants and animals within the same community is still doubted by some, chiefly workers who have not attempted to consider both elements of the biota in their studies.

In conclusion, the principal features embodied in the biome concept are, firstly, that plants and animals together constitute ecological communities, secondly, that the basic unit of biotic communities is the biome with its constituent climax associations as well as their developmental stages.

The biome is conditioned primarily by climate and secondarily by edaphic and other local conditions during its developmental stages. An essential feature of the organization within the biotic community is the element of interaction which is based upon the struggle for existence. The effect of the community and its constituents upon each other and upon the habitat creates a succession of stages which results in a more or less stable climax stage, the association. Associations composed of similar life forms and with similar ecological organization constitute a biome.

The concept that the community is an organism, while perhaps a useful adjunct, is not essential to the acceptance of the concept of the biome as representing a living dynamic ecosystem of living organisms, dependent in its climax stages not upon the habitat but upon climate.

REFERENCES

ADAMS, C. C. 1909—An ecological survey of Isle Royale, Lake Superior. Rept. Bd. Biol. Surv. Mich. 1908.

———1915—An ecological study of prairie and forest invertebrates. Bull. Ill. St. Lab. Nat. Hist. **11**:33-280.

ALLEE, W. C. 1927—Insect ecology. Ann. Ent. Soc. Am. **20**:439-444.

———1934—Concerning the organization of marine coastal communities. Ecol. Monogr. **4**:541-544.

BAKER, F. C. 1910—Ecology of the Skokie Marsh area, with special reference to the Mollusca. Bull. Ill. St. Lab. Nat. Hist. **8**:441-499.

BEED, W. E. 1936—A preliminary study of the animal ecology of the Niobrara Game Preserve. Bull. Conserv. Dept., Univ. Nebr. **10**:1-33.

BEI-BIENKO, G. YA. 1930—The zonal and ecological distribution of Acrididae in the west Siberian and Zaisian plains. (In Russian). Bull. Plant Prot., USSR, ser. I, **1**:51-90.

BIRD, R. D. 1930—Biotic communities of the aspen parkland of central Canada. Ecology **11**:356-442.

CARPENTER, J. R. 1936—Concepts and criteria for the recognition of communities. Jour. Ecol. **24**:285-289.

———1937—Fluctuations in biotic communities, III. Aspection in a ravine sere in central Oklahoma. Ecology **18**:80-92.

———1938—An Ecological Glossary. Univ. Okla. Press, Norman.

———1939—The grassland biome. (In preparation)

CLEMENTS, F. E. 1916a—Plant Succession. Carn. Inst. Wash. Pub. **242**.

———1916b—The development and structure of biotic communities. Printed Program, Ecol. Soc. Amer., New York meeting, Dec. 27-29, 1916, page 5. (abstract reprinted in Jour. Ecol. **5**:120-1, 1916).

———1934—The relict method in dynamic ecology. Jour. Ecol. **22**:39-68.

———1936—Nature and structure of the climax. Jour. Ecol. **24**:252-284.

COOPER, W. S. 1926—The fundamentals of vegetational change. Ecology **7**:391-413.

DAHL, F. 1903—Winke für ein wissenschaftliches Sammeln von Thieren. Sitzber. Gesell. naturf. Freunde Berlin **1903**:444-475.

———1908—Grundsätze und Grundbegriffe der biocönotischen Forschung. Zool. Anz. **33**:349-353.

———1921—Grundlagen einer ökologischen Tiergeographie. Fischer, Jena.

DAVENPORT, C. B. 1903—The animal ecology of the Cold Spring Sand Spit, with remarks on the theory of adaptation. Univ. Chicago Decennial Pubs., 1st ser., **10**:155-176.

DICE, L. R. 1922—Biotic areas and ecological habitats as units for the statement of animal and plant distribution. Science **55**:335-338.

FORBES, E. 1844—Report on the molluscs and Radiata of the Ægean Sea and on their distribution as bearing on geology. Rept. Brit. Ass. Adv. Sci. **12**:130-193.

FORBES, S. A. 1880—On some interactions of organisms. Bull. Ill. St. Lab. Nat. Hist. **3**:1-7.

———1907—On the local distribution of certain Illinois fishes: an essay in statistical ecology. Bull. Ill. St. Lab. Nat. Hist. **7**:273-303.

FREIDENFELT, T. 1925—Bemerkung über die Bedeutung und die Methoden einer mathematischen Prüfung von Mittelwerten, unter Berücksichtigung der Planktologie. Handbuch der biol. Arbeitsmeth. **9**(2).

FRIEDRICHS, K. 1927—Grundsätzliches über die Lebenseinheiten höherer Ordnung. Die Naturwissenschaften **15**:153, 182.

———1930—Die Grundfragen der land- und forstwissenschaftlichen Zoologie. Berlin.

———1937—Ökologie als Wissenschaft von der Natur, oder biologische Raum-Forschung. Barth, Leipzig.

GAMS, H. 1918—Prinzipienfragen der Vegetationsforschung. Ein Beitrag zur Begriffsklärung und Methodik der Biocönologie. Vierteljahrschrift Naturforsch. Gesell. Zürich **62**.

GEORGE-BARCLAY, H. 1924—The plant succession of the flood-plain of the Mississippi river with special reference to the pioneer stage. Thesis, Univ. of Minnesota Library (unpublished).

HART, C. A. & H. A. GLEASON. 1907—On the biology of the sand areas of Illinois. Bull. Ill. St. Lab. Nat. Hist. **7**:137-272.

HEFLEY, H. M. 1937—Ecological studies on the Canadian River floodplain in Cleveland county, Oklahoma. Ecol. Monogr. **7**:345-402.

HEROLD, W. 1928—Kritische Untersuchungen über die Methode der Zeitfänge zur Analyse von Landbiocönosen. Z. Morph. & Ökol. Tiere **10**:420-432.

JÄGER, G. 1874—Deutschlands Thierwelt nach ihren Standorten eingetheilt. Stuttgart.

JONES, G. T. 1926—Review of Pearse's Animal Ecology. Ecology **7**:503-504.

KASHKAROV, D. N. 1933—Environment and Community (Principles of Synecology). (In Russian). Biomedgiz, Moscow and Leningrad.

———1938—Principles of Animal Ecology. (In Russian). Medgiz, Moscow and Leningrad.

KATZ, N. J. 1933—Die Grundprobleme und die neue Richtung der Phytosoziologie. Beitr. Biol. Pflanzen **21**:133-166.

KRAUS, G. 1911—Boden und Klima auf kleinstem Raum. Fischer, Jena.

LANG, K. 1931—Faunistisch—ökologische Untersuchungen in einigen seichten Oligotropen bzw. Dystrophen Seen in Südschweden. Lund Univ. Årsskrift (2) **27**(18):1-173.

LEVANDER, K. M. 1914—Om undersökning av ett torvmarksområde ur topografisk-faunistik och ekologisk synpunkt. Meddel. Soc. Fauna & Flora Fennica **40**.

MININ, N. V. 1936—Division of the space of life in ecology. (In Russian; English summary). Prob. Ecol. & Biocenol. **1936**:61-67.

MÖBIUS, K. 1877—Die Auster und die Austernwirthschaft. Berlin. (Translated as "The oyster and oyster culture," Rept. U. S. Fish. Comm., 1880, **8**:683-751, 1883).

———1893—Ueber die Thiere der Schleswig-Holsteinischen Austernbänke, ihre physikalischen und biologischen Lebensverhältnisse. Sitzber. Kgl. Preuss. Akad. Wiss. Berlin **1893**(1):67-92.

NUTTALL, G. H. F. 1923—A review of the relationships between plants and animals. Am. Nat. **77**:449-475.

PALMEN, J. A. 1908—Plan för undersökning av fogelfaunan ur topografisk synpunkt. Helsingfors.

PALMGREN, PONTUS. 1928—Zur Synthese pflanzen- und tierökologischer Untersuchungen. Acta Zool. Fennica **6**:1-51.

PEARSE, A. S. 1926—Animal Ecology. McGraw-Hill, New York.

PETERSEN, C. G. J. 1913—Valuation of the sea, II. The animal communities and their importance for marine zoogeography. Rept. Dan. Biol. Sta. **21**:3-44.

——— AND P. B. JENSEN. 1911—Valuation of the sea, I. Animal life of the sea bottom and its food and quantity. Rept. Dan. Biol. Sta. **20**:1-79.

PHILLIPS, J. 1931—The biotic community. Jour. Ecol. **19**:1-24.

VON POST, H. 1867—Försök till iakttagelser i djur- och växstatistik (Versuch zu Beobachtungen in der Tier- und Pflanzenstatistik). Öfversikt af Kongl. Vetenskaps-Akad. Förhandlingar **1867**(2).

RUTHVEN, A. G. *et al.* 1906—An ecological survey in northern Michigan. Mich. Geol. Survey, Ann. Rept. **1905**:1-333.

———1911—A biological survey of the sand dune region on the south shore of Saginaw Bay, Michigan. Mich. Geol. & Biol. Surv., Pub. **4**, Biol. Ser. 2.

SCHMIDT, —. 1922—Biocönologie und Sociologie. Naturwiss. Wochensch. N. F. 21(58).

SEGERSTRALE, S. G. 1932—Quantitative Studien über den Tierbestand der Fucus-Vegetation in den Schären von Pellinge (an der Südküste Finnlands). Comm. Biol. Soc. Sci. Fennica **3**(2):1-145.

SHACKLEFORD, M. W. 1929—Animal communities of an Illinois prairie. Ecology **10**:126-154.

SHELFORD, V. E. 1906—Preliminary notes on the distribution of tiger beetles and its relation to plant succession. Biol. Bull. **14**:9-14.

———1911—Physiological animal geography. Jour. Morphology **22**:551-618.

———1912—Ecological succession, IV. Vegetation and the control of land plant communities. Biol. Bull. **23**:59-99.

———1913—Animal Communities in Temperate America. Univ. Chicago Press.

———1915—Principles and problems of ecology as illustrated by animals. Jour. Ecol. **3**:1-23.

———1926—Terms and concepts in animal ecology. Ecology **7**:389.

———1931—Some concepts of bioecology. Ecology **12**:455-467.

———1932—Basic principles on the classification of communities and habitats and the use of terms. Ecology **13**:105-120.

———*et al.* 1935—Some marine biotic communities of the Pacific coast of North America. Ecol. Monogr. **5**:249-354.

——— AND S. OLSON. 1935—Sere, climax and influent animals with special reference to the transcontinental coniferous forest of North America. Ecology **16**:375-402.

——— AND E. D. TOWLER. 1925—Animal communities of the San Juan channel and adjacent areas. Publ. Puget Sd. Biol. Sta. **5**:33-73.

SMITH, V. G. 1928—Animal communities of the deciduous forest succession. Ecology **9**:479-500.

TANSLEY A. G. 1935—The use and abuse of vegetational concepts and terms. Ecology 16:284-307.

TAYLOR, W. P. 1935—Significance of the biotic community in ecological studies. Quart. Rev. Biol. **10**:291-307.

THIENEMANN, A. 1918—Lebensgemeinschaft und Lebensraum. Naturwiss. Wochenschr. N.F. **17**(20, 21).

———1920a—Biologische Seetypen und die Gründung einer Hydrobiologischen Anstalt am Bodensee. Archiv für Hydrobiologie.

———1920b—Die Grundlagen der Biocönotik und Monards faunistische Prinzipien. Festschr. für Zschokke **4**:1-14.

THORNTHWAITE, C. W. 1931—The climates of North American according to a new classification. Geogr. Rev. **21**:633-655.

———1933—The climates of the earth. Geogr. Rev. **23**:433-440.

VAN DER KLAAUW, AND A. MEYER. 1936—Ökologische Studien und Kriticken.
I. Die Bedeutung der Teologie Kants für die Logik der Ökologie. Sudhoffs Arch. Gesch. Med. **27**:516-588.

II. Zur Geschichte der Definitionen der Ökologie, besonders auf Grund der Systeme der zoologischen Disziplinen. Ibid. **29**:136-177.

III. Zur Aufteilung der Ökologie in Autökologie und Synökologie in Lichte der Ideen als Grundlage der Systematik der zoologischen Disziplinen. Acta Bio-Theoretica **2**:195-241.

VEITZMAN, KH. S. 1936—Concerning some biocoenological concepts. (In Russian; English summary). Prob. Ecol. & Biocenol. **1936**:68-78.

VERRILL, A. E. AND S. I. SMITH. 1871—Report upon the invertebrate animals of

Vineyard Sound and adjacent waters. Rept. U. S. Fish. Comm. **1871-2**: 295-778.

VESTAL, A. G. 1913—An associational study of Illinois sand prairie. Bull. Ill. St. Lab. Nat. Hist. **10**:1-96.

———1914—The internal relations of terrestrial associations. Am. Nat. **48**:413-445.

WARMING, E. 1909—Œcology of plants. (English translation by Percy Groom). Oxford.

WEAVER, J. E. AND F. E. CLEMENTS. 1926—Plant Ecology. McGraw-Hill, New York.

WOODBURY, A. M. 1933—Biotic relationships of Zion Canyon, Utah, with special reference to succession. Ecol. Monogr. **3**:147-245.

UNIVERSITY OF OKLAHOMA,
NORMAN, OKLAHOMA.

DISCUSSION

Emerson: I am impressed with this analysis of large biological units like the "biome". At the same time I think before these subdivisions are fully understood we shall have to make very complete studies of the details of the integrating mechanisms between them. It reminds me of the earlier history of biology when an organ in the organism was found and was labelled the heart. Further analysis did not disprove that that organ was there but demanded a long series of intimate studies. Moreover there are concepts which may be studied in terms of quantitative differences also and which in the last analysis are statistical. For this reason I cannot approve of the mere study of the life cycle of individuals, since a phase of intimate relationships must be known in order to study these larger units. The larger units are not going to disappear once we known their intimate natures.

Gleason: We are all agreed that there exist in nature various aggregations of plants or animals or both which we may call communities. One of the principal points of difference among us is the choice of aggregations which is to be considered the biosociological unit. The speaker has taken for his unit the very large aggregation known as the biome and divided it into smaller parts. It is equally possible to consider a small community as the unit, and to combine them into larger categories.

MacGinitie: I am certainly very much in sympathy with the idea of the biome. But we can never separate any one thing from the rest since our definition of the environment includes everything. In some of the work done in San Francisco Bay Kofoid estimated the amount of plankton which was there as 10-12 tons per acre. It is generally considered that 1/10 may be animal life and the other 9/10 may be plant life. In my paper I could not consider the plant life because I was looking at it from the animal point of view. However, I do consider the plant life a very important part of the whole picture.

Park: There is something regarding the protocol which bothers me. Do the terms presented have objective reality?

Carpenter: In passing over a given area, I think that the divisions which are recognized in this system would be recognizable to the worker after he had studied the area.

Park: Has enough work been done to date to warrant the assignment of these terms?

Carpenter: Yes. I feel that the work we have done to date does warrant these assignments. Whether or not they could be divided into further units, I can not say.

Park: It seems to me that we must attach statistical or quantitative objectivity to these terms. Does the terminology have such implications?

Carpenter: In my mind it does.

Emerson: I wonder if this simile isn't instructive. The speaker has studied the anatomy of ecological grouping and the parts have been labelled.

Carpenter: This "anatomy" or structure is based on the two biomes which have been studied: the prairie and the coniferous forest. According to my experience, the same thing applies to the deciduous forest. Beyond that, I do not know.

Eggleton: Using this simile and carrying it still further, fresh-water habitats may be said to have this same anatomy, or structure.

Carpenter: The structure of a community is a little different from the question we have discussed here. The structure of any given community is an integral part of it. Another community of different requirements would have a different structure. This is the one thing which is common in most climax forms. In this sense, at least, the structure of some communities is comparable. This seems to be fundamental. Whether or not different communities have the same structure is a different question. The arrangement of the niches of aquatic communities may be different from that of terrestrial communities, but I believe that these arrangements are comparable.

Mottley: With regard to statistics, one deals with the two main phases, qualitative and quantitative. On the qualitative side of the picture qualitative terms are used to describe typical or modal conditions; in order to investigate the variations at the margin of these typical conditions quantitative methods should be used. The size of the unit should be adapted to the particular problem.

Carpenter: I agree. In the example of the prairie certain variations from the typical are found which are called faciations, etc. It is under these latter conditions that the quantitative methods are most valuable. A faciation, therefore, would in terms of a, b, c, and d, depend upon the total distribution of d.

Gleason: The association has been characterized by species, a, b, and c, while a, b, and c, plus d, are termed a faciation. Is it not possible to call the latter the association and the former the faciation?

Carpenter: It would depend on the total extent of the distribution of d.

Gleason: The faciation therefore depends on the size of the area rather than the difference in the species.

Carpenter: It depends upon its relationship with the total area. An effort was made to obtain species which are characteristic of the prairie as a whole and they are designated here as a, b, c. D may be characteristic of only a local area; therefore the rest of the prairie is not deficient of d. No species not characteristic of the prairie as a whole would be used to designate the whole.

Cain: The speaker's table shows a four dimensional structure. Where these subdivisions of the biome association are spread out chorologically two dimensions are involved. The layering, with superposed societies, constitutes a third dimension of components of the large group. In the form of layers, all societies occupy different ecological regions. Communities representing stages in succession give us the fourth dimension, that of time.

Mottley: What disposition is made of the question of time, daily variation, moment to moment variation, etc.?

Carpenter: Both seasonal and diel (or daily) variations are recognized and termed seasonal societies and diel phases. The moment to moment variations are included as gradual adjustment in the diel cycle, i.e., between phases.

Conard: I am pleased with the speaker's assurance that we may use the suffix "tion" without committing ourselves. I assume that the suffix "ies" does commit us to the idea of succession. It is a terminus which I have never used. The determination of that point is perhaps the last step in the study of a community. I am very much pleased also with the speaker's decision to name the prairie, not from the first piece which he happens to fall upon, but from one which he has carefully selected as representative of the central or typical condition. Plant sociology and the study of the community in general are likely to profit greatly by the decision not to name groups until the

predominant conditions have been determined. The subdivisions may be determined subsequently.

Lippmaa: The largest divisions of the vegetation of a continent as used by Clements may well be designated climaxes because they are actually more conditioned by climate than by the soil conditions. Yet in every formation great differences of its vegetation exist due to such factors as duration of snow cover, exposition, substratum (calcareous or siliceous rock, peat, sand, loam, water, etc.). Therefore, it seems to be better not to begin with the largest unit but rather with the smallest one. These remarks do not lessen the usefulness of the concept "biome". It is doubtful, however, whether or not the biome is "the primary unit of bioecology". Moreover not every community seems to be composed of both plants and animals.

Carpenter: "Primary" is used here with the meaning of "fundamental".

MacGinitie: It is easier to say that where animals are there are plants. Even in the depths of the ocean the animals present are dependent on the plants on the surface. In all cases known to me where animals live they cannot be separated from plants being dependent on them directly or indirectly. If the planktonic plants are eliminated all the surface animals underneath will die immediately.

Lippmaa: The problem of homogeneity has been studied carefully, e.g. by Raunkiaer, Nordhagen, Kylin et al. The frequency numbers are dependent upon three factors: 1) the number of individuals of a particular species, 2) the distribution of these within the community, and 3) their morphology (e.g., *Thymus serpyllum, Carex arenaria).* The greater the homogeneity of the community the smaller may be the size of the quadrat used in its analysis.

Mottley: Is it necessary to call the ecology of plants and animals bioecology?

Carpenter: I have used it here only to emphasize the fact that I am including both plants and animals. It is quite obvious that we will have, for some time at least, both schools of ecology working side by side in this country. It seems unfortunate that they should not be able to understand one another. I hope that some common denominator of measurement will be found which would enable one to translate one "language" into the other. For example, my "associations" are communities which are not recognizable in terms of the "association" of Braun-Blanquet. Frequently, as far as one school is concerned, the other school is apparently wasting its time, a very unfortunate situation.

Gleason: Should not those groups treated here as faciations be regarded as the fundamental units which are units and in turn component groups of a higher category?

Carpenter: The smaller units such as faciations do not conform to the behavior and distribution of the larger influent animals. Our large fundamental units must definitely take into account more important animals, such as the bison, deer, caribou, etc.

Steiger: De we know anything about the conditions of the prairie under the influence of the bison or do we draw conclusions from the inferences of cattle grazing?

Carpenter: No specific study has been made, but I suspect a strong parallel between the effects of cattle and those of bison. They are at least comparable. But the bison occurred in much greater herds than cattle does today. As a result the former probably had a much greater influence. But with very few exceptions the bison roamed over a large area and exerted its influence on any particular area but once in several years. The situation in most cattle ranges today is, unfortunately, very different.

MacGinitie: What were the original conditions? Is the bison being placed into a picture where he possibly does not belong?

Carpenter: Admittedly the picture today is changed from that of the original conditions. But that is why we try to obtain and to preserve the situations which we think most nearly approximated primeval conditions. Unfortunately we are about 150 years too late to get the whole picture.

The Individualistic Concept of the Plant Association

H. A. Gleason

The units of vegetation, which form the subject of our discussions this week, were just as easily visible to primitive man as they are to us today. They were equally visible to the sages of Greece and Rome two thousand years ago, to our European ancestors a thousand years ago. Through all these long years they were neglected by scientists, whose thoughts were turned in different directions, but they were recognized by the laity. As a result the languages of Europe all contain a number of terms which refer, usually rather loosely, to vegetation.

Certainly every botanist who studied plants in their natural habitat during the eighteenth century was familiar with many types of vegetation, but to them he gave little thought, possibly considering that they were not proper subjects for scientific investigation. To see vegetation units is one thing; to take cognizance of their existence, to investigate their nature, to become aware that they have structure and behavior which may be analyzed, to formulate a philosophy in explanation of them, are entirely different matters.

Four our purposes, and with the admission that many desultory references to vegetational units may be found in the works of earlier authors, we may say that the first definite, scientific discussion of the subject may be attributed to Grisebach, and we may repeat his often quoted words: Ich möchte eine Gruppe von Pflanzen, die einen abgeschlossenen Charakter trägt, wie eine Wiese, ein Wald, u.s.w., eine pflanzengeographische Formation nennen. This was in 1838, exactly a century ago, and we may congratulate ourselves that in this conference we are celebrating the centenary of the association-concept.

During the next sixty years, the study of vegetational units was sporadic, mostly superficial, and usually purely descriptive in nature. True, we can sometimes see in the literature of this period statements which may be interpreted as applying to the underlying philosophy of the association, but in most cases such statements are casual or accidental and do not indicate that the authors had given deep thought to the fundamental nature of the vegetation which they described.

Not until the advent of the twentieth century did botanists turn their minds seriously to the consideration of underlying questions. Since that time we have made great progress. We have developed methods for the exact observational study of the association. We have recognized conditions and processes in their development, their existence, and their disappearance, and these conditions and processes are quite unlike anything in the life-history of an individual plant or animal, so that our recognition of them has required the development of new habits of thought. We have described in modern terms vegetation from nearly all parts of the world. We have developed

systems of classification, by which the units of vegetation may be orderly arranged. We have invented and brought into accepted use a new terminology by which these conditions, processes, structures, and concepts may be described and discussed.

There is, however, one important question which has not yet been settled to the satisfaction of all concerned. This is the fundamental question, basic to all our work: What *is* a plant association?

Out of the thousands of pages of literature which have been used in expounding various views on the matter, three well marked theories may be chosen, and all others may be regarded as merely variants from them. These three are:

1. The association is an organism, or a quasi-organism, not composed of cells like an individual plant or animal, but rather made up of individual plants and animals held together by a close bond of interdependence; an organism, or a quasi-organism, with properties different from, but analogous to, the vital properties of an individual, including phenomena similar to birth, life, and death, as well as constant structural features comparable to the structures of the individual.

2. The association is not an organism, but is a series of separate similar units, variable in size but repeated in numerous examples. As such, it is comparable to a species, which is also composed of variable individuals. Under this view, the association is considered by some to be a concrete entity, merely divided into separate pieces, while by others the association as a whole is regarded as a mental concept, based on the common characters of all its separate pieces, and capable of typification by one or more of those pieces which most nearly approach the average or ideal condition.

3. The vegetation unit is a temporary and fluctuating phenomenon, dependent, in its origin, its structure, and its disappearance, on the selective action of the environment and on the nature of the surrounding vegetation. Under this view, the association has no similarity to an organism and is scarcely comparable to a species.

In the original paper, in which this idea was presented to the botanical public in 1926, it was called the individualistic concept, a term which may well be continued.[1]

Whether fortunately or unfortunately, my own work during these twelve years has been wholly taxonomic. Nevertheless, observation of numerous plant associations during my field work in this period has merely intensified my own belief in the fundamental truth of the individualistic concept. The exposition of the concept which follows is merely a re-statement of the subject in different terms; it is in no way different in principles or conclusions from the first presentation in 1926.

The argument for the individualistic concept rests on a series of theses,

---

1 Gleason, H. A. The individualistic concept of the plant association. Bull. Torrey Bot. Club **53**(1):7-26, 1926.

each of which is so obvious, so well known, so universally understood and accepted by all ecologists, that none of them requires prolonged discussion.

1. Every species of plant has reproductive powers in excess of its need.

The land surface of the world is already fully occupied by plants. Room for additional plants is made available only by the death of plants now existing. If seed germination were always perfect, if there was no mortality among plants before reaching their reproductive stage, it would be necessary for each existing plant to produce only one seed in order to perpetuate its species and to maintain the existing number of individuals. On the contrary, every species of plants produces a considerable number of seeds or other propagating bodies, often yielding an annual crop over a long period of years. Since the world is full of plants, it is a fact that, on the average, only one of them comes to a state of full maturity, but huge numbers of seeds or other propagules are capable of growth and ready to grow if favorable conditions are offered. A well kept lawn, for example, may produce very few weeds during the course of the summer, but if the lawn is plowed, the same expanse will promptly develop an astonishing crop of weeds of many species. The bottoms of drained ponds, the first season after drainage, produce many plants of terrestrial species. These and other examples of the same sort are so well known and so conspicuous that we may safely state that the surface of the world is heavily planted with an excess of seeds, most of which never develop, but many of which will develop if a favorable opportunity is offered.

2. Every species of plant has some method of migration.

The means of migration are well understood and require no discussion. The effectiveness of migration is often not appreciated. The distance to which some seeds may be carried by currents of water, by wind, or by birds is known to some degree, but the migration of other less favorably adapted species is also remarkable. Such seeds may be carried by rodents or ants or washed away by heavy rains. It is a demonstrable fact for all plants, without regard to their methods of migration, that more seeds are finally deposited near the parent plant than are carried to a great distance, the number decreasing, roughly speaking, inversely as the square of the distance. But effectiveness of migration is increased by various kinds of accidents and also by the known longevity of seeds in many species. We may therefore conclude, and our conclusion is supported by direct evidence familiar to all of us by personal experience, not only that the world is heavily planted with seeds, as stated under our first thesis, but also that these seeds come not only from the existing plants of the immediate vicinity, but also from plants at some distance. In any unit of vegetation the potentiality of plant production includes not only the natural species of this unit, but numerous species not now found in it and derived from other vegetational units of different character.

3. The environment in any particular station is variable.

Probably the simplest instance of variability which may be mentioned is light. Each day starts at midnight with light at or near zero. A little before

sunrise the light curve begins to rise, reaches a theoretical maximum at noon and drops to zero shortly after sunset. The length of the curve varies with the season, being longest in summer and shortest in winter; the amplitude of the curve varies in precisely the same way, reaching its maximum on June 22 and its minimum six months later. Any and all of the 365 curves which constitute a year's cycle may be subject to irregular reductions in amplitude by cloudy weather. Nor is the quality of the light constant, but varies somewhat with the altitude of the sun and the condition of the atmosphere. These are all relatively simple matters, but there are also variations due to sun-spots, and there may have been and in fact may still be variations due to changes in the inclination of the earth's axis or the eccentricity of its orbit, or to other causes even more remote and far slower in their action. Locally, for many plants the light is changed again by the shade of taller plants, and this shade varies in its effectiveness from hour to hour, from season to season, and as the shading trees grow taller, from year to year.

The variation in temperature of the surrounding air shows similar irregular variations superposed on cyclic progressions in a way quite similar to the variation in light. Soil moisture is more irregular, with abrupt rises followed by longer periods of decrease, and with great variability in the amplitude of the curves. Available soil moisture is another question, based primarily on the total soil moisture, but complicated by matters of temperature, acidity, and other abstruse conditions. Similar conditions hold for every other factor of the environment taken individually and with all of them taken collectively: they are complex and variable to the last degree.

A second class of environmental variations may be called fluctuations. They are illustrated by our irregular alternation of cold and warm, of dry and wet years, of late and early seasons.

Still a third class of variations is important in its effect on plant life, and includes cumulative environmental changes which progress over a period of years or centuries or ages. Such, for example, are the silting up of a pond, the deepening and widening of a ravine by erosion, the exhaustion of soil fertility by percolation of rain water, the accumulation of humus, the increase in temperature following the retreat of a glacier, or the decrease in rainfall in the rain-shadow of a mountain range during its elevation. Although excessively slow, the cumulative effect of these environmental changes is ultimately profound.

All three of these classes of environmental variation are in operation simultaneously in every situation. The first class is regular and predictable; the second class is irregular and unpredictable; the third class is slow and often immeasurable. The amplitude of the fluctuations in the second class is normally much greater than the steady progression of the third class. A single year of deficient rainfall may cause a greater change in the depth of water in a pond than fifty years of silting, or may have more effect on the crops of Montana than five thousand feet of additional elevation of the Rocky Mountains. If we assume that we are now approaching another advance of continental glaciers, the annual drop in temperature associated with it is far less

than the fluctuation from a warm to a cold year. Nevertheless, the only fundamental difference between the three classes is the factor of time.

4. The development of a vegetational unit depends on one or the other of two conditions, the appearance of new ground or the disappearance of an existing association.

The appearance of new ground is a matter of very little importance. More land may be added around the coasts of our continents by further elevation of the coastal plain or the building up of the shores by coastal deposits. More land may be added in supra-alpine regions by reduction of altitude through erosion. More land can not be added by increasing rainfall in deserts: our deserts are already fully occupied by plant life; some deserts merely support less plant life than others.

In the vast majority of cases, an association appears on the ground previously occupied by a different association. It makes no difference whether the earlier association is removed by the slow processes of ordinary succession or suddenly by some cataclysm. If the existing vegetation is destroyed by the axe, by fire, by a landslide or by hot lava, some plants go first and some go last. If the vegetation is changed by a slow process of succession, some of the original inhabitants still go first and some linger. In both cases, some plants of the next association, the pioneers, appear first and others are delayed. The only essential difference between them is the factor of time, greatly shortened in the first case, often greatly prolonged in the second.

The various factors which collectively constitute the environment of a plant may be separately measured and diagrammed, although often with much difficulty, but no one has ever succeeded in reducing to a single statement or a single equation the total environment of any plant. For practical purposes the only measure of the environment is its result, as expressed in plant life. An oak tree may easily live to be three hundred years old. Let us see what this implies concerning its relation to the environment. It means that through this whole period, in spite of its extraordinary variability, the environment has never once exceeded the limits tolerated by the living protoplasm of the tree. The weather has never been too hot or too cold, too wet or too dry; the soil has never been too acid or too alkaline; no environmental factor has ever been too much or too little, or if the limits have sometimes been surpassed, it was for a period too short to be fatal.

The clearest example of temporary excess is the annual cold winter, during which the activities of the oak sink so low that we call the tree dormant. The oak is not only able to adapt itself to the variations in environment, but is able to vary its own life processes enormously to meet such a critical condition as winter cold. Not every plant meets the emergency in the same way. Some herbs actually die, but are fortunate in producing a seed which is not killed by cold and which produces another generation the following summer. There are still other plants whose seeds are also killed by the cold. These plants do not live with the oak, or, of they do, they must be re-established every summer by fresh seeds from a more favorable climate. Such plants are familiar as

cultivated in our gardens. The canna and dahlia may flourish not far from the oak, but they disappear forever if not removed by us to a more favorable climate for the winter and replaced the following spring.

Now leaving these trite illustrations, which have been used merely to recall to our minds what we all know from common experience, let us consider the question from a broader standpoint. We at once arrive at the general theorem, that each plant seizes and uses the particular time-period during which the environment is in a condition suitable to it. When the environment passes these limits, the plant dies. For the old oak, this limit has not been reached for the three hundred years of its life and, so far as we can imagine, not for still longer periods in the past when preceding generations of oaks were growing on the same spot, nor will it be surpassed for many years in the future, during which the descendants of the present tree will be living there. For the dahlia, the limit is reached before the plant has completed a single generation: it is cut off in October while it still bears young leaves and unopened buds. During the same summer, the Galinsoga which infests our gardens in this vicinity may produce several generations. If our lives were measured by days instead of years, we can imagine an ecologist saying, "I have seen three generations of Galinsoga on this one spot of ground. Evidently we are dealing with a stable environment and Galinsoga will live here forever." He would be wrong. With our knowledge of vegetational conditions actually extending over about three centuries, we now say, "Oaks have occupied this spot of ground for three hundred years. Evidently we have here a stable environment and the oak will live here forever." If our lives were seventy centuries instead of seventy years, would we not see that we were again wrong? Like the short-lived Galinsoga, which utilizes the time period which we call summer, the long-lived oak is utilizing a longer time-period, and the time has been, and in the future will be again, when the race of oaks can no longer live on this particular spot.

During the time-period when a species may occupy a station, diverse effects are exerted upon the plants by the variable environment. Variations of the first type, which are regular, periodic, and uniform, such as night and day, winter and summer, act uniformly and unavoidably upon all plants. The physiological processes of every plant are adjusted to meet them. While their investigation forms an important part of plant physiology, their effect on plant distribution and their interest to the plant ecologist are negligible.

Variations or fluctuations of the second type, including such phenomena as cold and warm years, of dry and wet periods, of late and early seasons, have a pronounced ecological effect. This is evidenced in agriculture and horticulture by years of heavy or light yield, by the abundance or lack of pests and parasites, by the lateness or earliness of bloom or fruit, by the losses due to late frosts in spring or early frosts in autumn. If such fluctuation is maintained for even a few years, its results become so grave as to be of national importance, as shown recently by the effect of only four years of deficient rainfall in our Plains States.

The effect of these fluctuations on natural vegetation is precisely the same

qualitatively, but less pronounced quantitatively, since crop plants are deliberately introduced into a region, while natural vegetation has been adjusted to the fluctuations through previous experience. In natural vegetation, the effect of fluctuation in the environment is seen in phenological phenomena, in the amount of annual growth, in the vigor of individuals, in the number of seeds produced, in the number of seedlings produced, and therefore in the relative number of individuals. These fluctuations rarely last very long, seldom affecting more than a single year; they therefore rarely cause the disappearance of a species or the appearance of a new one.

That fluctuations of environment affect the relative number of individuals of a species is a fact which has rarely been demonstrated in research in pure ecology, since accurate quantitative studies of vegetation have seldom been repeated in the same area over a series of years. I have personal records from the same area taken at varying intervals over twenty years and can assure you that they show conspicuous variations in the number of individuals of some species, and scarcely none for other species. We may assume that the physiological processes and environmental demands of the latter are so broadly adjusted that no fluctuations have ensued of sufficient magnitude to affect the plants. In the former group we may also assume that their physiological processes are more strictly defined or that the normal environment is already off the optimum for the species, so that fluctuations do interfere demonstrably with the number of individuals. Abundant records of this phenomena are available through the careful observations on our grazing lands. Here the environmental fluctuation is largely in the number of animals feeding on the plants, but the effect is precisely the same. Differences in grazing lead immediately to the reduction of certain species and the multiplication of others.

The rare disappearance of a species because of environmental fluctuation is probably due to the fact that the fluctuations of any one year have been repeated at various times in the past, and species which would be exterminated by them have already been removed. Nevertheless, the long period of drought recently ended in the western states will probably have this effect in many instances, although I am not able to cite any single example at the present time.

The relatively rare appearance of a new species for the same cause, is due primarily to the time-factor involved in plant migration. Environmental fluctuations are of relatively short duration; migration of plants is slow and before additional species can reach the spot, migration has been stopped by the return of the environment to normal. If next winter were to be omitted and summer temperatures should continue for another twelve months without interruption, we still could not expect to find mangroves along the shores of the north Atlantic. Sufficient time must always be allowed for the reaction of plants to any environmental change.

The variations of the third type, the slow-moving, long-continuing environmental changes caused by physiographic processes, geological developments, or climatic changes, cause no directly observable or measurable effect on vegetation, at least in most cases. In these days the effect of erosion during a single

year can sometimes be measured or estimated but it has taken a century for it to make an impression on our minds. The silting of a pond with the resultant changes in plant life is also fairly rapid, so that it has sometimes been observed and recorded by a single person during his own lifetime. Even in these relatively rapid examples, and of course in the slower variations of climate, the effect of the change is always masked by the wider amplitude and quicker action of the fluctuations just discussed. Nevertheless, these fluctuations are based on a norm, and if the norm itself varies the amplitude of the fluctuations tend always to abate in one direction and to extend in another.

Suffice it then to repeat that on every spot of ground the environment is continually in a state of flux, and that the time-period in which a certain environmental complex is operative is seized on by the particular kinds of plants which can use it. The vegetation of every spot of ground is therefore also continually in a state of flux, showing constant variations in the kinds of species present, in the number of individuals of each, and in the vigor and reproductive capacity of the plants.

With this idea of the time-period in our minds, let us look back to the origin of some hypothetical association, which is now populated by three species, designated X, Y, and Z. This association originated in one of two ways, on new and denuded ground bare of plants, or in replacement of a preceding association.

In the former case, of denuded or new ground, species X, Y, and Z must have been derived from some neighboring area or areas, and these must have been within migrating distance. In this neighboring area species X, Y, and Z may or may not have been living together. In these original stations the environment was variable, their seed production was variable, and the migration of these seeds was controlled largely by those inexplicable factors which we call chance. Some times, possibly seldom or possibly frequently, their seeds were carried to this particular spot of ground which we are considering. On this spot of ground the environment was also variable, and in this variation a certain time-period began which permitted the growth of species X, Y, and Z. Their seeds happened to be available, as association of X, Y, and Z appeared, and the time period during which it may continue has not yet ended.

If our hypothetical association appeared in succession to some preceding association, the circumstances are still similar. The plants of the earlier association, which we may designate A, B, and C, eventually reached the end of their time-period and disappeared. Their disappearance may or may not have been simultaneous. The particular environmental changes which facilitated the entrance of X, Y, and Z may not have been the changes which caused the loss of A, B, and C. The former may have entered first, so that at one time the association consisted of all six species, or entry and disappearance may have been more or less serial, so that the association passed through successive stages of A, B, C; X, B, C; X, Y, C; and finally X, Y, Z.

In either case, whether the association developed *de novo* or as a stage in succession, the variations of the environment may have been such that the

permanent entry of X, Y, and Z was preceded by shorter time-periods during which one or some of them was temporarily present. In short, any number of different sequences may be imagined, all based on variation in the environment and on the species then available through the chances of migration. As a further generalization we may also postulate that species J, K, and L, although adapted to the new environment, did not enter because their nearest stations were beyond the reach of migration; that M, N, and O did not enter because of the chance failure of migration, but may be expected to appear at any time; and that P, Q, and R actually migrated into the area but were unable to utilize the environment.

I have seen this variable result of the interaction of migration and environment beautifully illustrated along the shore of a lake, where winter storms and ice action keep the shore denuded of permanent vegetation. Each spring some storm washes on the beach a long strip of flotsam, twigs, fragments of bark, and dead leaves, and in it seedlings develop. Some years the strip of drift is marked by hundreds of seedlings of willow, at other times by seedlings of elm, and again by seedling red maples. In each case the environment is the same. The difference is caused by migration. If the flotsam is deposited at the particular time when maple seeds are falling in quantity, maple seedlings appear. A difference of a week or two in time results in willows, or in elms, or in no plant life at all.

Under ordinary circumstances, the annual fluctuations of environment are not sufficient to cause any profound or permanent change in the vegetation. Their effects are shown in the size and vigor of individuals or by changes in the relative number of individuals of different species. Only when the fluctuations reach a certain maximum or minimum do old species disappear or new species appear. But in the meantime the slow long-term variations in climate are still in operation and are cumulatively important in environmental selection.

An excellent example of these conditions became apparent during my early work in northern Michigan. Thousands of acres were then covered with a virgin forest of the so-called climax type, with beech, maple, and hemlock as the dominant trees. Of beech and maple there were millions of young trees, ranging from seedlings to tall specimens of the second story of the forest. But there were no seedling hemlocks, except in rare cases; all the hemlocks were mature trees, mostly 300-350 years old. About the beginning of the seventeenth century there had been some sort of an environmental change. Since that time the old hemlock trees had not died, but new hemlock trees had not been established. Another century or less would probably have caused the disappearance of the old trees, and the hemlock would have almost disappeared from the forest. Was that change of three centuries ago a mere fluctuation which has not yet returned to the normal, or was it the accretion of a climatic change to such a stage that it permanently passed the limit of tolerance of the hemlock?

In spite of this exception, I am quick to recognize that the effects of environmental change is less apparent in eastern America and western Europe, where most of our ideas on the association-concept have developed, than in

certain other parts of the world. Our vegetation is composed very largely of perennial species, and even the herbs are generally of long duration. That means that these species are already adjusted to all ordinary fluctuations of the environment, so that the vegetation persists with relatively little change through cycles of high or low temperature, or of excessive or deficient rainfall.

But in other parts of our country, where the vegetation is largely annual, fluctuations in environment are followed immediately by a reaction in the plant life. In the Mohave desert, rains at the proper season induce a great development of the desert annuals, which sometimes carpet large expanses of the land with a sheet of color. Species appear which have not been detected before and rare species become common. The next year, if it fails to receive rain at the critical time, may see the display replaced by mere bare areas of desert.

For ordinary plants, rooted to one place in the ground, environmental selection depends wholly on excess seed production and migration. But many animals, gifted with powers of voluntary locomotion, are continually selecting their environment or being selected by it. No such animal is restricted to any biotic association unless it alone affords him his necessary environment. The scarlet tanager, an inhabitant of the forest canopy, appears in my garden in town when cherries are ripe, and disappears when they are eaten. Migratory birds choose a new environment twice a year. The turkey buzzard of our southern states, except in its nesting, belongs to no biotic association, but enters any one in which it finds a temporary food supply.

The development of a new biota on any spot is therefore the result of environmental selection from the available population of adjacent areas. Similarly, the continuation on any spot of ground of what we have been pleased to call a biotic association is also due to the interaction of the same causes, available population and environmental selection.

While we may all admit the validity of this statement, one argument will immediately come to mind which will seem at first to minimize its importance, namely, that the changes in environment which I have mentioned are so slight that they produce relatively little effect. It is a fact that the majority of individuals of perennial plants continue through environmental fluctuation, because of the well known fact that a mature plant can successfully withstand conditions which would be fatal to seedlings or would prevent the germination of seeds. It is also a fact that plants are themselves a part of the environment, and their persistence always tends to reduce the effect of a variation in the physical environment. It is not until a reduction in their vigor or in their number has broken their environmental control that the full effect of an environmental change can be seen. The individualistic concept does not postulate annual changes of great magnitude, it merely emphasizes that a fixed and definite vegetational structure does not exist.

Another objection which may be brought forward is that the argument of a continuously fluctuating or steadily progressing environment, or both, can scarcely be reconciled with the sudden successional transitions from one associ-

ation to another. This has already been answered in part, when it was stated that mature plants can withstand conditions impossible for their seedlings. When finally, as the result of cumulative changes, the environmental control of the mature plants is broken, the consequent change in the total vegetation is rapid and profound. In this connection it must also be remembered that the theory of sudden steps in succession is largely based on the abrupt transitions in space between different associations. As a matter of fact, these narrow transition lines are more apt to indicate a high degree of stability of vegetation than a rapid rate of succession. . In each of the adjoining associations variation in vegetational structure is always active, along the lines stated by me already, but the absence of cumulative progressive changes in environment, together with a high degree of environmental control by the plants, leads to narrow and well-defined lines between them.

All the statements which have been made so far concerning environmental variability have purposely been restricted to variation in one spot during the course of time.

Variability of environment may also be correlated with space. In time-variability, the environment changes from one time to another on the same spot. In space-variability, environment differs from spot to spot at the same moment. The idea is so axiomatic, so familiar to all, that it scarcely needs any discussion, yet some generalizations may be desirable before we attempt to relate the condition to the individualistic concept.

Space variations are in many ways analogous to time-variations, both in their nature and in their effect. Analogous to the fluctuations of environment in time, which fluctuations are comparatively uniform over a reasonable amount of space, are the abrupt fluctuations in space. These, as is well known, are mostly correlated with the soil, in its chemical and physical properties, its elevation, slope and exposure. It must be repeated that these are fluctuations in space, and emphasized that they are relatively constant on any one spot through a reasonable period of time. Such fluctuations are often of extreme importance to plant life. In any region, they tend to show a wider amplitude of variability than do time-fluctuations.

There are also gradual variations in environment, so gradual, in fact, that their effect can not be observed by comparison of adjacent regions. Such are the variation in mean temperature, in average rainfall, in length of growing season, in length of day and night. Between two adjacent regions, the difference in these conditions is so slight that they are concealed by the far greater and locally more important fluctuations mentioned in the preceding paragraph. But they are cumulative, and it is probably impossible to draw a line 500 miles long anywhere in the United States, certainly in the north-south direction, along which these climatic variations do not cumulate to such an extent as to cause a marked difference in the vegetation at the two ends of the lines.

The selective effect of space-variation on plants is very similar to that of time-variation. To any spot of ground come seeds of various species of plants. Those seeds which find in the spot the environmental conditions which they

demand germinate and as adult plants become an integral part of the association. The population varies from place to place in a manner and to an extent determined by the variation in the environment. The population is chosen by environmental selection from the available immigrants.

There is nevertheless one important difference. In a time-series, the surrounding population remains relatively constant. From year to year it affords the same group of species from which immigrants may be drawn. In a space-series, the surrounding plant population may vary greatly from one end to the other. Not only is the environment different, but the immigrating species are also different and the resulting environmental selection is different.

Furthermore, time is always necessary for an environmental variation to exert its full effect on plant life. Fluctuations in time are often of short duration and have passed before their full effects can be realized. Fluctuations in space, on the contrary, are of relatively long duration, and on each spot the full effect of environmental selection can be reached.

In summary it may be stated that environment varies constantly in time and continuously in space; environment selects from all available immigrants those species which constitute the present vegetation, and as a result vegetation varies constantly in time and continuously in space.

Those who disagree with the individualistic concept will very properly raise at this time certain questions, based on facts which at first thought seem to invalidate the whole concept. Before these questions are stated here, so that their obvious implications may be refuted, two general statements may be introduced.

First, an association, or better one of those detached pieces of vegetation which we may call a community, is a visible phenomenon. As such it has dimensions and area, and consequently boundary. While its area may be large, the community is nevertheless a very tangible thing, which may be mapped, surveyed, photographed, and analyzed. Over this area it maintains a remarkable degree of structural uniformity in its plant life. Homogeneity of structure, over a considerable extent, terminated by definite limits, are the three fundamental features on which the community is based. Without these three features, Grisebach would never have published his statement of a century ago; without them, all our studies of synecology would never have been developed. Also, besides its extent in space, every community has a duration in time. Uniformity, area, boundary, and duration are the essentials of a plant community.

Second, every community occupies a position in two series of environmental variation. In the space-series, as the community exists *here*, in this spot, it is part of a space-variation, and its environment differs from the adjacent communities. In the time-series, as the community exists *now*, at this time, it is part of a time-variation and in its environment differs from the communities which preceded it or will follow it.

The individualistic concept postulates a continuous variation in space and

time. How can we reconcile this with the admitted uniformity in space and time?

In any community of reasonable extent, the variation of rainfall, temperature, length of day, and similar factors from one end to the other is extremely small. Not only is their effect proportionately small, but this effect is overshadowed by the much greater seasonal fluctuation. Soil, also is often uniform over the whole community, and when it it not uniform but varies significantly within small distances, we are prone to overlook its effects and to classify the variable vegetation in a single community. More important still, the dominant plants, which are distributed over the whole area of the community, exert such a uniform effect on the other species that discrepancies in the physical environment are more or less smoothed out or obliterated.

Nevertheless, it is difficult or impossible to find in any community two quadrats which are precisely similar. The community is a complex or mosaic of slight irregularities, all of which blend into an entirety of apparent homogeneity. We have all known of this lack of perfect uniformity, and have endeavored to evade it by developing the concept of a minimal area, but we have failed to realize its significance as indicating the general variability of vegetation.

Cumulative progressive changes in environment are generally so slow in their development that they make no pronounced effect from one year to the next, while the wider swings of fluctuating environment are so short in their duration that their full effect is not experienced. Also, comparatively few observers have kept careful records of vegetational change over a series of years. Furthermore, as in space variation, environment control by plants tends to overshadow environmental variation. Nevertheless, succession, which is merely vegetational change, is accepted by all as a fact; exact statistical records, when available, do show continuous variations in structure, and in many locations complete vegetational changes have occurred within the experience of a single observer.

The postulated uniformity of the community is therefore far from absolute. A community is uniform, either in space or in time, only to a reasonable degree. This uniformity is sufficient to enable us to recognize the community and to accept it as a unit of vegetation, while its variability, although slight, is sufficient to indicate the impossibility of considering any such area of vegetation as a definitely organized unit.

If vegetation varies continuously in space, how can we explain the abrupt transitions from one community to another, which are so conspicuous a feature of natural vegetation in many regions?

Abrupt transitions are in every case correlated with abrupt variations in the environment or with abrupt differences in the immigrating plant population. Some abrupt changes in environment are due to physical conditions, notably the soil, which may change notably within a short distance. The other changes are due to environmental control of the physical factors by the plant life itself. These account for most of the abrupt transitions in the eastern

states, or in any other region where a dense vegetation is possible. The sharp demarcation of zones around a pond or bog, for example, is caused almost entirely by vegetational control.

Abrupt differences in immigration exist only in areas which have recently been disturbed, such as an abandoned field, a lake shore recently worked over by waves, a ballast heap or a tract of newly filled ground. In such places the accidents of immigration often lead to the temporary establishment of distinct patches of vegetation, each characterized by one or a few species. Continued migration tends to smooth out these irregularities in a short time; environmental fluctuation favors certain species over others; denser growth leads to environmental control by certain species, and in the course of a few years such patchwork vegetation has blended to a relatively homogeneous community.

If vegetation varies continuously in space, how can we account for the repetition of the same vegetation in many separate communities?

The answer to this question is simple. There is no exact repetition of the same vegetation from one community to the next. There is an approximate repetition only.

It is a fact that in any region several to many examples of vegetation may be found in which the differences are so slight that they are not observed, or if observed are considered as unimportant and negligible. In any community absolute homogeneity is impossible, and the observed heterogeneity may well be due to chance. But in a single community, if it is large enough, differences between two ends may be discovered. Every ecologist who has undertaken quantitative analysis of vegetation will probably agree with this statement. I once examined two adjacent sections, each an exact mile square, of virgin hardwood forest. The soil was uniform and level and there was no surface drainage system, nor any indication of wetter and drier parts. Careful quantitative studies in each section showed conspicuous differences, not important differences, to be sure, which could not be explained by any visible feature. At the Biological S[t]tion of the University of Michigan, the aspen association, with a single continuous community some six miles long, exhibits demonstrable variation from one end to the other, with no visible reason.

Between two different communities, not too far removed from each other, the observable differences in structure are of essentially the same degree of magnitude as these fluctuations within the same community, and one may easily tend to credit them also to the effect of chance. But part of them, possibly only a small part, is due to the space-variation in the environment, and another part, again possibly small, is due to a difference in the available plant population upon which environmental selection operates. If a series of communities are observed at successively greater distances, these differences cumulate, so that those at the ends of the series may be strikingly different, although connected by imperceptible or apparently negligible intermediates.

One short-coming of our ecology has been that our field work has generally been confined to a small area. We have investigated and described all the associations in a small area, instead of trying to trace a single association

over its whole extent. In any small area, environmental variation, essentially repeated in many spots, produces several well-marked types of environment, each characterized by a similar vegetation. We justifiably draw the conclusion, from this limited evidence, that association-types are definite. But as soon as we extend our observations, we begin to realize that each separate community is merely one minute part of a vast and ever-changing kaleidoscope of vegetation, a part which is restricted in its size, limited in its duration, never duplicated except in its present immediate vicinity and there only as a coincidence, and rarely if ever repeated.

In other words, the similarities between adjacent communities, which have led to the views that the association is analogous to a species, or analogous to an organism, are not perfect similarities. They are caused by *nearly* similar environmental selection, intensified by *nearly* similar environmental control, from a nearly similar population. In addition to the imperfections of similarity caused by chance, and largely masked by them, are other variations of a cumulative nature. These, increasing in importance and in conspicuousness as more distant communities are considered, finally lead to vegetation of such unlike nature that they would never be classed in the same association-type.

In my original paper on this subject I mentioned as an example the alluvial forests along the Mississippi River and its tributaries over a stretch of about a thousand miles from its mouth to the northward. From mile to mile these forests show no considerable change; over a space of a hundred miles the changes may or may not be of ecological importance and the more important differences are apparently due to lack of time for sufficient migration to smooth out the variation. Yet these differences cumulate. One by one species disappear; one by one other species appear, and by the time one has reached, say, Indianapolis, there has been an almost complete change in the appearance and composition of the forest. Or, if the observer swings more to the west and travels up the Missouri and the Platte, he can see the disappearance of species one by one without corresponding replacement, until the forest is reduced to a fringe of willows and finally disappears completely in western Nebraska.

Within the state of Michigan, the beech-maple climax forest, always considered to be a definite, well distinguished association-type, exhibits profound changes from one end of the state to the other.

I also venture to say, without personal experience to verify the opinion, that even more remarkable transitions might be discovered elsewhere. For example, the forests of the foothills of the Rocky Mountains in Colorado, composed there largely of *Pinus ponderosa*, might be traced northward with similar gradual variation, thence eastward along the northern boundary of the grassland in Canada, and again southward to the forests of Illinois, and lead us to the extraordinary conclusion that the *Pinus ponderosa* forests of Colorado represent the same association as the *Quercus velutina* forests of Illinois and the aspen groves of Manitoba.

Over such distances as the three I have mentioned the flora from which

any area may be populated changes greatly. Such environmental factors as temperature, rainfall, and length of growing season also vary greatly and to an extent that completely surpasses the local fluctuatione between any adjacent communities. With the vegetation determined by environmental selection from the available plant population, and with both of these underlying features altered, obviously the resultant vegetation must also be entirely changed.

It must be remembered that we admit the essential uniformity of vegetation within a single community, and the frequent striking uniformity between adjacent communities. But the fact that these small cumulative differences do exist is basically important in the consideration of the general concept of the plant-association. They indicate that each community, and for that matter each fraction of one, is the product of its own independent causative factors, that each community in what we now choose to call an association-type is independent of every other one, except as a possible source of immigrating species. With no genetic connection, with no dynamic connection, with only superficial or accidental similarity, how can we logically class such a series of communities into a definite association-type? Truly the plant community is an individualistic phenomenon.

Every species of plant and animal migrates, whether as a mature individual, as many species of animals, or as a reproductive body, as the vast majority of plants. Among animals, migration is simetimes selective in its direction and goal, as illustrated by birds which follow definite routes to definite established breeding grounds. With other animals and with all plants, migration is purely fortuitous. It progresses by various means, it brings the organisms into variout places and to varying distances, but only those organisms which have reached a favorable environment are able to continue their life. Into this favorable environment other species also immigrate, and from all of the arrivals the environment selects those species which may live and dooms the others.

In this migration each migrating body acts for itself and moves by itself, almost always completely independent of other species. The idea of an association migrating *en masse* and later reproducing itself faithfully is entirely without foundation. Those cases in which there is a semblance of such a condition are caused by the proximity of the original association and the advantage which its species therefore have in migration. Even then, certain species always precede and certain others lag behind.

Summary

1. The ordinary processes of migration bring the reproductive bodies of a single plant or a species of plant into many places.

2. The ordinary processes of migration bring the reproductive bodies of various plants into the same place.

3. Of the various species which reach one spot of ground, the local environ-

ment determines which may live, depending on the individual physiological demands of each species separately.

4. On every spot of ground, the environment varies in time, and consequently the vegetation varies in time.

5. At any given time, the environment varies in space, and consequently vegetation varies in space.

6. A piece of vegetation which maintains a reasonable degree of homogeneity over an appreciable area and a reasonable permanence over a considerable time may be designated as a unit community. Within such an area and during such a period similarity in environmental selection tends toward similarity in vegetation.

7. Since every community varies in structure, and since no two communities are precisely alike, or have genetic or dynamic connection, a precisely logical classification of communities is not possible.

Although a summary is generally considered to close a discussion, it nevertheless seems desirable to indicate very briefly the relation of the individualistic concept to other current philosophies of the plant community.

The individualistic concept is totally at variance with the idea that the association is an organism, represented by many individuals, and also does not admit an analogy or homology between the species and the association. While affirming the existence of definite communities, characterized by reasonable uniformity over a considerable area terminated by a definite boundary, the concept denies that all vegetation is thus segregated into communities.

The concept is by no means opposed to the recognition of the synusia, or union, defining it as a group of plants whose physiological demands are so similar that they are regularly selected by the same environment and consequently regularly live together.

If classification of communities on the basis of floristic resemblance is rejected, and if broader areas of vegetation are searched for characters indicating genetic or dynamic similarity, these are first found in the broad floristic group now known as a biome. The plants of a biome, living together now as their ancestors have lived together and evolved together in the past, represent an environmental selection of a broad type, while lociation and faciation within the biome indicate the variability of the environment and the irregularity of migration.

DISCUSSION

Lippmaa: Though the theses of the speaker are acceptable the same can not be said of his conclusion that it is "impossible to choose any one phase of the vegetation as typical." The environment does not vary *continuously* in time and space. Abrupt changes caused by the differences in rock and soil composition, exposure, water supply, etc. are not uncommon. To such changes as well as those factors listed by the speaker effecting the development of vegetation must be added other eminently important ones such as the competition between the species composing the community and the time necessary for the stabilization of the community.

As regards "the exact repetition of similar vegetation" it is clear, that the units used in phytosociology are of a different kind than those of taxonomy. For the fundamental unit of taxonomy—the species—could hardly be considered "exact" by the chemist.

Gleason: Most of these remarks do not differ essentially from anything which I have said. The first topic regarding variation may require brief explanation. The curve, in which periods of slow and rapid variation alternate, still represents continuous variation.

In my early work I tried to read all the works on descriptive ecology dealing with American vegetation. I could scarcely find any two regions which contained the same associations. Conard's paper illustrated the same variability since he reported a Brometum in western Europe and England which has twenty-nine variants. These are almost certainly an expression of such cumulative differences in structure. In every small region, association-individuals may be found which are sufficiently alike to encourage us to classify them together, but extension of observation over greater areas shows that the small observed differences cumulate into important differences.

Emerson: It is useful to break down the larger categories into their units. It is also useful to build the units into larger wholes. I think by the same logic could be proven that the concept of the individual and of the species presents the same difficulties as the concept of the association. Is it not true that the biological integration of units is as real as the units?

Gleason: It was brought out in several places in my paper that the biological control by existing plants is an important feature of the environment.

Emerson: The speaker showed that each community is an individual, but I think it is also necessary to put them together again.

Gleason: The species are present, and these groupings of plants into communities exist. What I hoped to bring out here was that the particular grouping of plants is not found duplicated elsewhere. There are similarities among stands, or slight differences from stand to stand, and if you trace an association those little differences are cumulative.

Emerson: That is also true of the individual. A research taxonomist talks about species and races. Does the concept of a human race have meaning?

Gleason: I think the concept of race does have a meaning which is merely complicated by the intermediate forms, but we have no genetic relation or connection between these plant communities.

Emerson: One of the first principles of genetics is the reassortment of genes and chromosomes. I do not think the only reality is the individual and that the associations are not real integrated units.

Steiger: I agree with everything the speaker said about these variations in time and species, but all that is true of every living being. Plants are living beings and as such they do not possess the same degree of exactness, as NaCl for instance. Apparently we need a terminology.

Gleason: A classification of plant communities is certainly needed to enable us to talk about them conveniently.

Steiger: However, I would not compare an association with an individual. Even the comparison with the species is limited.

Spieth: As a taxonomist I do not like to hear associations compared with species. Any herring caught is going to have 60-65 vertebrae but it can not be predicted how many it is going to have. I think that is a very fundamental difference between the two.

Conard: I certainly enjoyed the speaker's analysis very much and I do not see any way of opposing his logic. Comparison of the association with the species has been stoutly opposed, but I feel that the same logic rules out the use of such terms as "species" or "human being". We are too different to be classified. It seems to me both from my own personal feeling and from reading the results of the work of others where the association as understood in the international sense has been used that there has been nothing in ecological inquiry which has been so fertile and so productive of results as the idea of the association. It is therefore so useful that whether logical or not, I am for it.

Gleason, Jr.: One can not deny the objective reality in a stand of vegetation any more than the objective reality in the daisy. But if all the daisies in the world were brought to some one location, that collection would be something very different from the concept of *Chrysanthemum Leucanthemum*. The latter is conceptual and purely subjective and very different from the other which is a specific collection of all the individuals which we have classified. There is a difference between human beings and *Homo sapiens*. The former have an objective reality, but the latter does not exist except in the mind of man. The same is true of any classification of vegetation. The vegetation exists and each individual stand exists, but the classificatory category exists only in the mind of man.

Emerson: I can not allow these remarks to go unchallenged. I think that the species has objective reality as well as the individual. If you say that "Homo sapiens" is a figment of the mind, I think you will be forced by logic to say that we are all individually figments of the mind.

Gleason, Jr.: I am certainly an aggregation of cells and a reality but the category obtained by classifying those cells is different from that aggregation, and is purely subjective. Modern logic has recognized the great importance of differentiating between a class and its components. The two have an entirely different logical value, and must be treated differently. Other treatment brings about the confusion of terms on which many well known paradoxes rest.

Emerson: The individual is a population of cells.

Gleason, Jr.: There is a distinction between a population of cells and a class of cells. A class of cells is an abstraction characterized by a quality, which is held in common by all those cells. That I think is fundamental.

Gleason: One can combine things of different nature and still have a concrete reality. When one classifies things he arranges them according to similarities. Philosophers agree that the development of a classificatory group leads always to an abstract concept.

MacGinitie: It seems to me that the speaker will have some trouble in limiting his defense from the other side. Why did he stop where he did? I do not like it for that reason.

The Unistratal Concept of Plant Communities (the Unions)

Theodor Lippmaa

For the development of the plant communities of an inhabited country two factors are of prime importance: 1) the existing flora, and 2) the available habitats. Moreover, each of the species found has its own requirements of temperature, light, water, etc. (Warming-Graebner, 1918; Lundegårdh, 1925; Braun-Blanquet, 1928, a.o.).

In the following diagram the horizontal lines indicate the limits within which all operative factors (water, pH, etc.) of a given habitat may vary without killing the particular species. There is no doubt, that the problem of

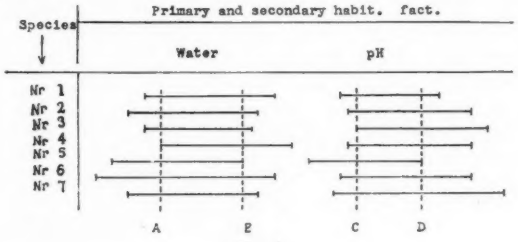


Fig. 1.

these limits is very complex. Thus, for instance, it is often not as important to know the lowest possible temperature of the habitat of a species as it is to know the number and seasonal distribution of days with a temperature below 0° C. Actually, each species has its specific requirements as is invariably shown, e.g., by attempts at acclimatisation.

Kotilainen (1928) studied the relations between the acidity of moor peat soils and vegetation, and found that, e.g., *Carex globularis* never occurs on peat with an acidity of less than pH=4, whereas *Menyanthes trifoliata* occurs within the limits of pH 4-5.5, and *Cypripedium calceolus* requires subneutral soil (the limit on the acid side is pH=6), etc.

It is unlikely that even two species can be found which agree exactly in all their habitat requirements. If, e.g., species 1-7 (Fig. 1) occur together, and hence their roots occupy the same soil horizon, the water content of the soil must be somewhere between a and b and the pH between c and d. Thus the range of fluctuation of a given factor of the habitat in regard to a plant community is always less than the amplitude of fluctuation of the same factor for the extreme species of the same community (Olsen, 1921; Kotilainen, 1928).

A permanent decrease or increase, for instance, in the water content of the habitat makes the habitat unfit for some species which are readily eliminated. As a rule they are replaced by other species of the available flora for which the change was favorable. Thus the floristic composition of the community changes gradually.

Another factor of great importance is the competition among the species of a community (Cajander, Sukatschev) which influences considerably the structure of communities. In the North competition ordinarily leads to the dominance of one or a few species in the community. In addition to the reciprocal influence of the species of a given community the influence of the species of adjacent communities certainly is also effective. They furnish spores, grains, and fruits which are brought in by wind, animals, etc. and act as intruders. Chance too plays an important rôle in the development of plant communities (Kujala, 1925; Palmgren, 1925) hence identical habitats may often present floristic differences in different stands of the same community.

Consequently the development of plant communities depends, in addition to the factors named above, on the following: 3) competition among species, and 4) chance. Lastly 5) time represents a factor able "to bind" the community to its habitat. A species can exist for a short time under conditions which are no longer suitable for it. Where the tense struggle for life begins, only a limited number of species of the available flora can exist. The outcome of competition is often greatly influenced, sometimes entirely changed, by animals and man (e.g., apophytic and anthropochorous communities, cf. Lippmaa 1933b, p. 150). Ultimately, a homogeneous plant community results which is in equilibrium with the habitat. In my opinion, such vegetation, i.e. vegetation in the state of equilibrium must be the first object of phytosociological research.

How are different plant communities recognized in the field? Many years ago Kujala pointed out the great difference between the boundaries of stands and those of patches which are unstable changing from year to year. Patches can change their place entirely over a longer period of years as, for instance, those of *Thymus serpyllum*. In the pine forests of Estonia, in dry sandy places, the moss layer is formed by *Cetraria islandica, Cladonia silvatica, C. rangiferina, C. alpestris,* etc. In some stands these lichens form motley mixtures, in others they occur isolated in more or less extensive patches of one species. Yet all those patches belong to the same community.

On the low sandy sea-coast with loamy underground the following communities are well developed in Estonia: (1) *Juncus Gerardi* community, (2) *Salicornia herbacea* community, and (3) *Festuca rubra* community. The first two are pronouncedly halophilous, being found only under the aggregations of cast up *Fucus* and their habitat being inundated during storms.

In the *Juncus Gerardi* community the sod is mostly continuous, though scattered holes of bare ground are present in which the sea water remains for a long time. But gradually the water disappears by evaporation and the ground is covered by a thin saline crust. Such areas form the habitat for the *Salicornia herbacea* community. Above these communities occurs the *Festuca*

rubra community, affected differently by the sea-coast since its habitat is rarely flooded once or twice a year.

The floristic composition of these communities differs as follows:

	Juncus Gerardi commun.	Festuca rubra commun.
Juncus Gerardi	5.5	--
Centaurium erythraea	2.1-2	+.1
Odontites litoralis	2.1-2	+.1
Plantago maritima	1.2	+.1
Triglochin maritima	1.1	+.1
Festuca rubra	--	5.5
Ophioglossum vulgatum	--	2.5
Potentilla anserina	--	2.2
Vicia cracca	--	+.1
Rhinanthus major	--	+.1
Leontodon autumnalis	--	+.1
Carex panicea	--	+.1
Glaux maritima	+.1	--

Phytosociologists disagree on the question of patches and stands, for some consider every different patch in the vegetation an individual stand. But all European phytosociologists agree that the *Juncus Gerardi* community and the *Festuca rubra* community are two easily distinguishable and well characterized communities, despite some common species, both being hemicryptophytic with some therophytes admixed and exposed essentially to the same climatic conditions (light, wind, precipitation).

These hemicryptophytic communities are relatively homogenous, consisting as a rule only of the herb layer and lacking a distinct moss layer. Homogeneity has often been regarded as an essential character of phytosociological units (communities) especially by Nordhagen (1928), who says: "It can readily be maintained that phytosociology would be impossible without the existence in nature of homogeneous or relatively homogeneous overgrown areas."

In one-layered communities, vegetation homogenous from the standpoint of the dispersion of individuals and species may often be homogenous also in its dominant life-forms. In several-layered communities, however, vegetation with a pronounced hypodispersion of species and individuals (hypodispersion is an indication of homogeneity) is often extremely heterogeneous as regards the distribution of life-forms within the community.

In the principal large-leaved deciduous forest association of Estonia, the "Nobilifrondetum herbosum," (Fig. 2) the following one-layered communities may be distinguished:

A
1. Ulmus-Acer-Tilia community
2. Corylus avellana community
3. Ribes alpinum-Lonicera xylosteum community
4. Hepatica triloba-Pulmonaria officinalis community

B
5. Rhytidiadelphus triquetrus-Eurhynchium striatum community
6. Anomodon longifolium-Isothecium myurum community
7. Neckera—Leucodon—Lobaria community
8. Parmelia sulcata—P. physodes community
9. Ramalina fraxinea—Evernia prunastri community

The floristic composition of the *Ulmus - Acer - Tilia* mesophanerophytic community is as follows:

	Life-form	Cover in 5-graded scale on sample plots of 400 m²				
Tilia cordata	MM	4	2	3	4	3
Ulmus montana	MM	3	3	--	2	3
Acer platanoides	MM	+	+	1	1	+
Sorbus aucuparia	MM	1	+	1	1	+
Populus tremula	MM	1	+	--	--	+
Corylus avellana	MM	--	2	2	+	--
Pyrus malus	MM	--	+	--	--	--
Betula verrucosa	MM	--	+	1	--	--
Salix caprea	MM	--	--	+	1	--
Quercus robur	MM	--	+	--	--	--
Fraxinus excelsior	MM	--	--	--	--	+

Fig. 2. Deciduous lime-tree forest on the Island of Abruca (Estonia).

The arborescent stratum, reaching over 25 m. in height, has an almost complete coverage and its minimal area is about 400 sq. m.

Although the microphanerophytic *Corylus avellana* community is hindered in its development in the shade of the *Ulmus-Acer-Tilia* community it assumes great importance when the tree layer is destroyed. This is true also of the nanophanerophytic community formed by *Daphne mezereum*, *Lonicera xylosteum* and *Ribes alpinum*.

The author studied the *Hepatica triloba-Pulmonaria officinalis* community in 30 stands throughout Estonia. The biological spectrum of this community is as follows:

Percentage distribution of species among life-forms

	S	E	MM	M	N	Ch	H	G	HH	Th
64	--	--	--	--	--	6.0	61.2	28.3	--	4.5

The minimal area is about 20 sq. mi.

Floristic composition

Characteristic species:

Actaea spicata L.
Allium ursinum L.
Asarum europaeum L.
Asperula odorata L.
Bromus Beneckeni (Lge.) Syme
Dentaria bulbifera L.
Hepatica triloba Gilib.
Lamium galeobdolon (L.) Crantz.
Lathraea squamaria L.
Mercurialis perennis L.
Milium effusum L.
Orobus vernus L.
Pulmonaria officinalis L.
Sanicula europaea L.
Stellaria holostea L.
Viola mirabilis L.

Companion species:

Aegopodium podagraria L.
Agropyron caninum P. Beauv.
Anemone nemorosa L.
Anemone ranunculoides L.
Athyrium filix femina (L.) Roth
Brachypodium silvaticum R. et Sch.
Calamagrostis arundinacea Roth
Campanula trachelium L.
Carex digitata L.
Chaerophyllum aromaticum L.
Dryopteris filix mas (L.) Schott.
D. Linnaeana C. Christ.
D. phegopteris (L.)C. Christ.
D. Robertiana (Hoffm.)C. Christ.
D. spinulosa (Müll.) O. Kuntze
Epilobium montanum L.
Equisetum pratense Ehrh.
Equisetum silvaticum L.
Festuca gigantea Vill.
Fragaria vesca L.
Geranium robertianum L.
Geranium silvaticum L.
Geum urbanum L.
Lactuca muralis (L.) Fres.
Luzula pilosa (L.) Willd.
Lycopodium annotinum L.
Majanthemum bifolium F. W. Schm.
Melampyrum silvaticum L.
Melica nutans L.
Moehringia trinervia Clair.
Oxalis acetosella L.
Paris quadrifolia L.
Poa nemoralis L.
Polygonatum multiflorum All.
Primula veris L.
Pteridium aquilinum Kuhn.
Pulmonaria officinalis L.
Pyrola minor L.
Pyrola secunda L.
Ranunculus cassubicus L.
R. lanuginosus L.
Rubus saxatilis L.
R. ideaeus L.
Solidago virgaurea L.
Stachys silvatica L.
Stellaria nemorum L.
Trientalis europaea L.
Urtica dioeca L.
Vicia sepium L.
Vicia silvatica L.
Viola mirabilis L.

The *Rhytidiadelphus triquetrus-Eurhynchium striatum* community occurs scattered in isolated patches on the ground, on stones, etc.; sometimes it is wholly absent or nearly so.

The floristic composition is as follows:

	I	II	III	IV	V1
Rhytidiadelphus triquetrus	3.2–3	3.2–3	5.4	+.2	3.2–3
Eurhynchium striatum	3.2–3	2.2–3	+.1	5.3	2.2
Mnium undulatum	1.1–2	+.1	+.1	1.1–2	2–1–2

1 Estonia, Island Abruka; size of sample plots 2 sq. m.

Plagiochila asplenioides	+.1	--	+.2	--	+.1
Rhodobryum roseum	+.1	+.1	+.1	+.1	+.1
Mnium medium	--	+.1	—	--	+.1
Hylocomium proliferum	--	+.1	+.1	--	--
Dicranum scoparium	--	+.2	--	--	--
Dicranum majus	--	--	+.2	+.2	--
Thuidium recognitum	--	--	+.1	--	--
Pleurozium Schreberi	--	--	+.1	--	--
Cirriphyllum piliferum	--	--	+.1	+.1	+.1
Mnium cuspidatum	--	--	--	+.2	--
Brachythecium rutabulum	--	--	--	+.2	--
Mnium stellare	--	--	--	+.2	--

This community is a pure community of "bryochamaephyta reptantia." Owing to the small size of its components, the minimal area of this clinging community differs profoundly from that of the rooted communities of the forest and approaches that of the following epiphytic communities on trees (6-9, p. 117).

The tree stumps are occupied by the *Anomodon longifolium-Isothecium myurum* community of the following floristic composition:

	I	II	III[1]
Neckera complanata Hüb.	3.2–3	2.2	1.2
Anomodon longifolium Bruch	2.2	5.5	3.2
Isothecium myurum Brid.	--	--	1.2
Homalia trichomanoides Br. eur.	--	+.2	+.2
Thuidium recognitum Hedw.	1.2	--	--
Thuidium tamariscifolium Lindb.	+.2	--	--
Mnium cuspidatum Leyss.	+.2	1.2	+.2
Brachythecium rutabulum Br. eur.	1.2	+.2	+.2
Eurhynchium striatum Schimp.	+.2	--	--
Homalothecium sericeum Br. eur.	--	1.2	--
Rhodobryum roseum Limpr.	--	--	+.1
Leucodon sciuroides Schw.	--	1.2	+.2
Anomodon viticulosus Hook. et Tayl.	--	1.2	--

1 Estonia, Island Abruka; size of sample plots about 1 sq. m. I—on *Populus tremula*. II—on *Ulmus montana*. III—on *Acer platanoides*.

The *Anomodon longifolium-Isothecium myurum* community rises from the ground to about 50-70 cm. This community is likewise composed entirely of "bryochamaephyta reptantia" and has some species in common with the *Rhytidiadelphus triquetrus-Eurhynchium striatum* community of the ground layer.

From about 70 cm. to the upper part of the crowns the trunks and branches are covered with two lichen communities and an aggressive moss community (*Neckera-Leucodon-Lobaria* community). The competition between this community and the lichen communities always ends in favour of the aggressor.

Floristic composition:

	Tilia cordata (2m²)	Ulmus mont. (2m²)	Ulmus mont. (2m²)
Leucodon sciuroides Schwaegr.	5.5	5.5	3.2–3
Lobaria pulmonaria (L.) Hoffm.	+.1	2.2	3.2–3
Neckera complanata Hüb.	--	--	+.2
Mnium cuspidatum Leyss.	--	+.2	--
Homalothecium sericeum Br. eur.	2.1–2	+.2	--
Hypnum cupressiforme L.	+.2	+.1	--

This community of "bryochamaephyta reptantia" rises on robust trunks and branches of old trees high into the crowns.

The dominating epiphytic vegetation at a height from 2-3 m to 5 m is formed by the *Parmelia sulcata-P. physodes* community.

	Ulmus montana Im	Tilia cordata Im	Betula ver. Im
Parmelia sulcata Taylor	2.2–3	2.2–3	3.2–3
Parmelia physodes (L.) Ach.	--	+.2	2.2
Physcia pulverulenta (Hffm.) Nyl.	1.2	--	--
Parmelia fuliginosa (Fr.) Nyl.	+.2	+.2	--
Radula complanata Dum.	+.2	--	--
Parmelia subaurifera Nyl.	--	--	+.2
Frullania dilatata Dum.	+.2	--	--

Here the foliose life-form dominates. From 5-6 m. to the highest part of the crowns the *Parmelia sulcata-P. physodes* community meets strong competition from the photophilous *Ramalina farinacea-Evernia prunastri* community. The floristic composition of this community is as follows:

	Ulmus montana Im	Tilia cordata Im	Salix caprea Im	Corylus avellana Im	Populus tremula Im
Ramalina farinacea (L.) Fr.	2.2	3.1–3	2.2	+.2	3.1–2
Evernia prunastri (L.) Ach.	+.1.2	1.2	+.1	3.2	3.1–2
Ramalina calicaris (L.) Fr.	+.2	3.1–2	4.1–3	+.2	--
Anaptychia ciliaris (L.) Mass.	3.2–3	--	+.1	--	+.2
Ramalina populina (Ehrh.) Wain.	1.2	+.1	1.1	--	--
Usnea spp.	--	+.1	+.1	1.2	--
Alectoria implexa (Hoffm.) Nyl.	--	+.1	--	--	--
Lobaria pulmonaria (L.) Hoffm.	+.2	--	+.2	--	+.2

All communities just described are well characterized floristically and by their particular habitats. Groups A and B have no common species. As to group A, even there the differences in the floristic composition between communities 1, 2, 3 and 4 are so great, that no common species is found in the records, although they occur sometimes. The communities of the lower layers may contain the seedlings and immature plants of a higher stratum. Such a progeny of the plants of a higher stratum is called "transgressive" in the community of any inferior stratum (Cain, 1934, p. 533).

When compared with the example given on p. 114, the differences between the superimposed communities 1, 2, 3 and 4 are much more considerable than, for instance, those between the *Juncus Gerardi* association and the *Festuca rubra* association (cf. p. 113).

Although the differences between the communities in group B are not so sharp as in group A, they are nevertheless distinct enough. In any case, they are no less prominent than in the sea-coast communities previously described.

The preceding analysis is based upon the concept of one-layered associations formulated by the author some years ago (Lippmaa, 1933). The one-layered associations are defined as follows:

> The elementary units of homogeneous and relatively stabilized vegetation (i.e. in equilibrium with the habitat) are one-layered associations, characterized by a definite floristic composition and by their ecology. The bulk of the species of a one-layered association belongs to the same or two related life-forms.

Although Du Rietz, Gams, Kujala, and Regel repeatedly pointed out the heterogeneity of many-layered associations, the many-layered method is applied today almost everywhere in the analysis of many-layered vegetation such as shrubby communities and forests. The Sixth International Botanical Congress, Amsterdam, 1935, recommends "to use the term 'association' for vegetation-units characterized mainly in the sense of Zürich-Montpellier plant sociologists, or at least for units of the same order of sociological value."

Thus the recommendation of the Third Botanical Congress (1910) is changed essentially. The proposal of Flahault and Schröter, accepted unanimously in Brussels, reads as follows: "An association is a plant community of definite floristic composition, uniform conditions of habitat, and uniform physiognomy. It is the fundamental unit of synecology." Moreover it was pointed out clearly by Flahault and Schröter that the association is not a topographic unit since the same locality may include many associations, and that the ecology of the associations rests upon the life-forms of its species. When compared with the definition of the one-layered associations just given, the definition of Flahault and Schröter may appear very similar.

Actually the association of Flahault, Schröter, Adamovic, Beck v. Mannagetta, Briquet, Drude, Engler, Harshberger, Smith, Warburg, and Warming differs in the case of many-layered vegetation from the author's concept, as may be seen from the remark of Flahault and Schröter (1910, p. 25) that "many associations, especially shrubs and woods are composed of several layers."

As already stated, the term "association" was recommended by the Amsterdam Congress for the fundamental unit of the phytosociologists of Zürich-Montpellier. Braun-Blanquet and Pavillard (1928) characterize this unit as follows: "Chaque association, l'unité sociologique fondamentale, se reconnait floristicuement par son ensemble spécifique et principelment par ses espèces charactéristiques. Les espèces différentielles peuvent être utilisées pour distinguer des association pauvres en espèces caractéristiques. Pour caractériser plus complètement et pour mieux accentuer l' unite de l'association on peut utiliser toutes autres catégories de caractères écologiques, génétiques, chorologiques." An association in the sense of Braun-Blanquet and Pavillard may

be very heterogeneous as to life-forms: succulents, epiphytes, phanerophytes, chamaephytes, hemicryptophytes, geophytes, therophytes, bryochamaephytes, etc. may occur together.

The question arises: what designation should be used for "one-layered association?" The following comparison may be useful to elucidate the fundamental differences of the "one- and several-layered methods."

A		B	
Science	Fundamental unit	Science	Fundamental unit
chemistry	element	systematic botany	species
mineralogy	mineral	plant synusiology	union (1-layered association)
petrography	rock	plant sociology	association

For a geologist the different rocks are units by means of which the surface of a given area is analyzed. In plant sociology the associations (according to Flahault, Schröter, Braun-Blanquet, Pavillard etc.) are the fundamental units by which the vegetation is analyzed. A rock may be simple (e.g. rocksalt) or composed of many minerals (e.g. granite); likewise an association may consist of a single union (one-layered association, e.g. *Verrucarietum maurae*) or of several unions (e.g. *Fagetum silvaticae*).

The parallelism in groups A and B is evident and it is imperative to choose a new term for "one-layered association." This term—*union*—was proposed by Du Rietz and Gams (1935) and is now accepted also by the author.

Consequently an association may consist of either one union [*Verrucaria maura* ass. (Häyren), *Scitonemetum crassi* (Rübel), etc.] or of several unions [*Fagetum silvaticae, Lauretum nobilis, Laricetum pratosum* (Rübel)]. As much as a knowledge of minerals is indispensable to a successful study of rocks, a complete investigation of an association requires likewise a knowledge of all the participating unions.

As the number of existing rocks exceeds greatly the number of existing minerals, so the number of associations surpasses by far the number of unions on the earth.

The simplicity of unions regarding layering is emphasized here, since they are always based on the dominance of a single or of two related life-forms.

In the Russian steppes, besides the dominating element composed of perennial tufted grasses such as *Stipa* spp., *Festuca sulcata, Koehleria gracilis*, etc. ("components" according to Paczoski), there occur therophytes like *Eragrostis poaeoides, Setaria viridis, Echinopsilon sedoides*, etc. ("ingredients"). In dry years only components are present; in rainy summers the ingredients appear more or less numerous. The community of components is very different from the ingredient community in floristic composition, in the dominating life form, and in ecology. The ingredients and components belong certainly to different unions, although they occur in the same stratum.

Similar periodically separated unions are well known from the desert regions (cf. Lippmaa, 1938, p. 8).

Thus far the *range* of a plant community has scarcely ever been determined. Most plant sociologists are engaged in the study of the vegetation of a more or less limited area. However, a knowledge of the range of a plant community is of no lesser value than that of a single species.

The range of a union may be determined by direct phytosociological analysis on an area of sufficient extension. Investigations of this kind, which often must extend over a whole continent or more, cannot be carried out without a great measure of international collaboration which does not exist today.

In my opinion, there is another way which leads to the goal. For the determination of the range of the union the ranges of its "characteristic species" or of its "constants" which occur in the union on a given area may be used. Furthermore, the whole floristic literature, fortunately very rich, may be consulted.

The list of characteristic species and constants of the *Galeobdolon-Asperula-Asarum* un., as far as they occur in Estonia, is given on p. 115. There the local facies of the union is called the *Hepatica triloba-Pulmonaria officinalis* community.

The results of this investigation (Lippmaa, 1938) may be summarized as follows:

The areas of the species concerned fall into different groups as distinguished below.

A. Species with European distribution (some of them with isolated areas in Asia).

Actaea spicata L.
Allium ursinum L.
Anemane nemorosa L.
Asarum europaeum L.
Bromus Beneckenii (Lge.) Syme
Carex digitata L.
Dentaria bulbifera L.
Lamium galeobdolon Crantz
Lathraea squamaria L.
Mercurialis perennis L.
Sanicula europaea L.
Stellaria holostea L.
Pulmonaria officinalis L.

B. Species with isolated areas in Europe and Eastern Asia.

Asperula odorata L.
Hepatica triloba Gilib.

C. Species with Eurosiberian range.

Orobus vernus L.

D. Species with Eurasiatic range.

Fragaria vesca L.
Majanthemum bifolium (L.) F. Schm.
Melica nutans L.
Oxalis acetosella L.
Paris quadrifolia L.
Rubus saxatilis L.
Viola mirabilis L.

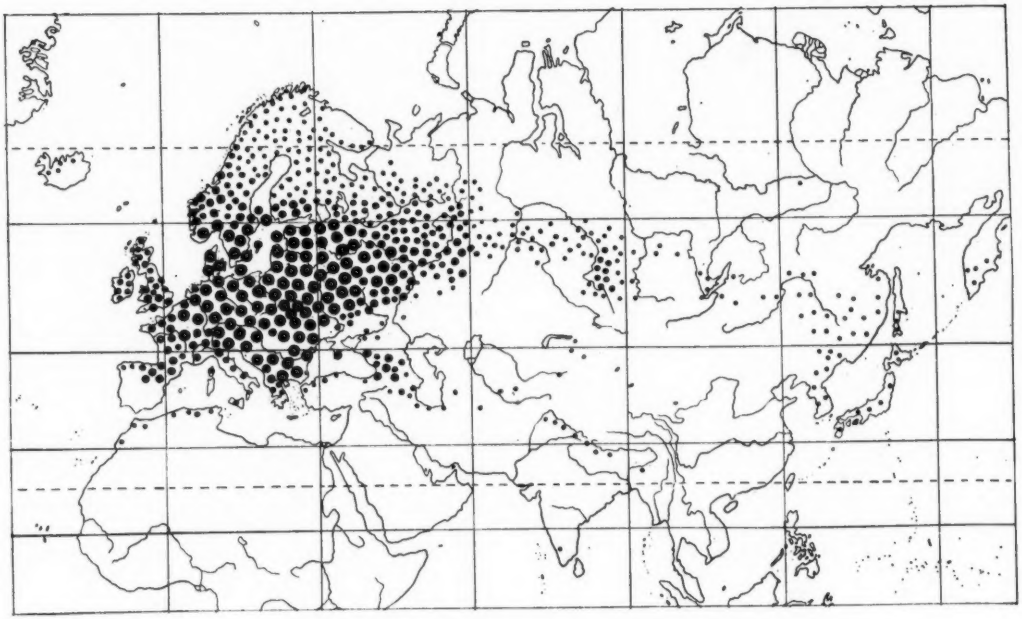


Fig. 3. The range of the Galeobdolon-Asperula-Asarum union.

E. Species with Eurasiatic-boreal American range.

Milium effusum L. *Trientalis europaea* L.

It is an old and as yet undecided question whether the recognition of plant communities should be based upon the constants or upon the characteristic species. Therefore, it is interesting to attempt the determination of the area of the union in two ways; first, from the characteristic species and second, from the constant species.

In both cases the method is identical. The distribution of each species in question is indicated on cards by dots. Then all data are entered on a single card divided into areas of 2.5° longitude and 2.5° latitude. Thereupon the number of characteristic species or constants represented by one or more dots in each area is ascertained.

Fig. 3 represents the range of the *Galeobdolon-Asperula-Asarum* union obtained by using the characteristic species. The dots are of four classes. The smallest ones (I) indicate 1 to 4 species; (II)—5 to 8 species; (III)—9 to 12 species, and (IV)—13 to 16 species.

As may be seen, the *Galeobdolon-Asperula-Asarum* union is a European union. Yet it is not easy to say where the boundary of its range lies, since it loses gradually, both northward and southward, one characteristic species after another. But what is the *lowest* percentage of characteristic species permitting the recognition of the union as still present? Obviously only a conventional limit can be found. If the accepted lowest percentage is 50 per cent in Fig. 3, only dots of sizes III and IV would indicate the range of the *Galeobdolon-Asperula-Asarum* union.

Its range covers Central and Eastern Europe from southern Scandinavia and southern Finland to northern Italy and the Balkans, and extends from southern England and western France to the River Volga. There are some isolated areas in the southern Ural, the Caucasus, the Crimea and the Altai (ne... Kuznetsk in the Alatau Mountains).

The forests of this part of Europe are relatively well known and described permitting a ready check of the range thus determined. The results obtained coincide perfectly with those presented above and complete them in many respects.

The union is luxuriantly developed in the Balkans as is evident from the investigations of Stojanoff (1932). The number of species in the union is twice the number present in Estonia. Four facies can be distinguished: the Adriatic f., the Hellenic f., the facies of the central Balkan, and the Pontic facies. They are all characterized by some particular species. In the Crimea (cf. Poplawskaja 1929 and Wulff 1932) a particular facies, the Crimean facies, must be distinguished. It is characterized by the abundance of *Cephalanthera rubra, Dentaria quinquefolia* and *Euphorbia amygdaloides* and some

other species. This facies is related to the Kolchic facies of the Caucasus as may be seen from a comparison with the results of Koschewnikow (1935, 1937). The peculiar species are: *Trachystemon orientale, Paeonia triternata, Dentaria quinquefolia, Festuca drymeia, Paris incompleta, Cyclamen ibericum, Asarum ibericum.*

The Central European facies, extending even into Hungary (cf. Soo 1927), is widely distributed in Central Europe (Switzerland, Austria, Czechoslovakia, Germany, Denmark, southern Sweden). It is characterized by such species as *Melica uniflora, Arum maculatum, Ranunculus lanuginosus, Aruncus silvester, Lysimachia nemotum, Prenanthes purpurea, Potentilla sterilis, Elymus europaeus,* etc. All species characteristic of the union in Estonia occur there also. Many analyses of this facies are found in contributions of Soo (1927), Braun-Blanquet (1932), Waldo Koch (1926), Gams (1927), Vierhapper (1932), Domin (193?), Klika (1936), Kujala (1936), Markgraf (1932), Meusel (1935), Lindquist (1932), Ostenfeld (1932). England and western France possess the Atlantic facies of the union, which contains *Scilla nonscripta, Helleborus foetidus, Hypericum androsaemum,* etc. (cf. Watt and Tansley 1932). Significant is also the lack of *Asarum europaeum, Hepatica triloba, Viola mirabilis, Orobus vernus, Bromus Beneckenii* and *Pulmonaria officinalis.*

For eastern Europe the following facies are characteristic: the northern f., the Balto-cassubian f., and the Sarmatic f. The northern facies occurs on the Åland Islands. It is relatively poor in species and is characterised by the lack of *Lamium galeobdolon, Asperula odorata* and *Mercurialis perennis.* The Balto-cassubian facies occurs in Poland, Latvia, Lithuania, Estonia, and the USSR. The floristic composition of the Balto-cassubian facies is given on p. 115. It has been studied by Szafer (1932), Paczoski (1929), Klika (1930), Kujala (1936), Regel (1933), Lippmaa (1932, 1933, 1935), Rühl (1936), Linkola (1929), Kupffer (1931), Ganeschin (1927), Fleroff (1899). The Sarmatic facies in Eastern Russia was studied by Korshinsky (1888). It contains such species as *Corydalis cava* ssp. *Marschalliana, Dentaria quinquefolia, Lilium martagon* which do not occur in the Balto-cassubian facies. The bulk of species is identical in both facies, only some important species of the latter are missing (e.g. *Allium ursinum, Sanicula europaea, Lamium galeobdolon, Hepatica triloba*).

Particularly interesting is the isolated area occupied by the Altaic facies. It was studied by Krylow (1891). There the union is more poorly developed than elsewhere. Nevertheless, it contains 66 species, half of them occurring also in the Balto cassubian facies. Particular species are: *Anemone altaica, Geranium albiflorum, Corydalis bracteata, Osmorrhiza amurensis, Crepis lyrata,* etc.

The relation between the existing facies may be represented by the following scheme:

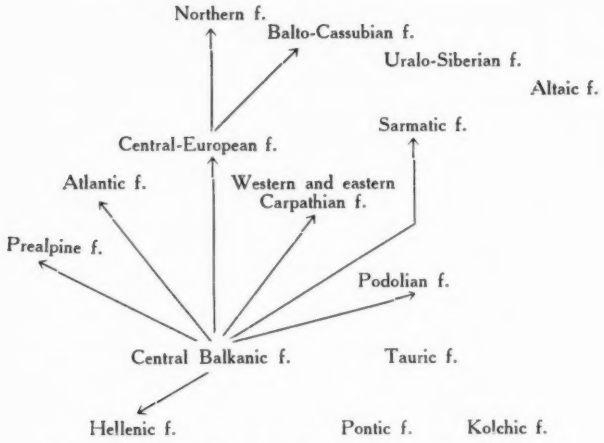


Fig. 4. The facies of the Galeobdolon-Asperula-Asarum union.

This scheme reveals the key position of the central Balkanic facies. To explain this fact and many others the relationship of the characteristic species of the union must be studied. In this connection only the characteristic species occurring in the union in Estonia are taken into consideration.

1. *Actaea spicata* L. s.str. (=*A. spicata* L. var. *nigra* Willd. f. *typica*) is a European species with isolated stations in Western Siberia (Tobolsk, Kuznetski Alatau). According to Krylow, *A. spicata* in these Siberian stations is a Tertiary relict. Very nearly related is *A. acuminata* Wallich which occurs in Austria, Hungary, Yugoslavia, and after an enormous gap, in the Himalayan Mountains, Tibet and eastern Asia. Other species are: *A. erythrocarpa* Fisch. from Scandinavia to China; *A. pachypoda* Ell., *A. rubra* (Ait). Willd. and *A. alba* (L.) Mill. in North America. All species are very closely related.

2. *Allium ursinum* L. (sect. *Ophioscordon*) is an isolated European type representing a Tertiary woodland plant.

3. *Asarum europaeum* L. is a European species distributed from Atlantic Europe (there rare!) to the Ural Mountains. Isolated relic stations occur in Siberia (Tobolsk, Kuznetski Alatau). The Caucasus has a related species—*A. ibericum* Stev. A great number of species is described from China (ca. 25 spec.), fewer from North America [e. g., *Asarum canadense* L., *A. virginicum* L., *A. macranthum* (Schuttl.) Sm., *A. arifolium* Mich., etc.]. *A. europaeum* L., as a Tertiary plant (Engler 1879), stands wholly isolated in the present European flora.

4. *Asperula odorata* L. is widely distributed in Europe from England to

the Ural. In Siberia it occurs only as a relic in isolated stations (e.g. Kuznetski Alatau). It occurs also on Saghalin and in Japan. The Asiatic range is represented by many scattered areas and is evidence of a wider distribution in the past. In the subsection *Galioideae* of the genus *Asperula, A. odorata* stands isolated. According to Diels (1918), the species belongs to the group which he calls *aperiodic;* he emphasizes that the family *Rubiaceae,* by its development, is essentially tropical in distribution.

5. *Dentaria bulbifera* L. is a European species with a range from England to the Caucasus and from southern Finland to Italy. The genus, unquestionably Tertiary, contains about 20 species which occur in Central and southern Europe, the Caucasus, China, Japan and North America (*D. laciniata* Muhlenb., *D. heterophylla* Nutt., *D. maxima* Nutt., *D. diphylla* Michx.). Siberia has as a very rare Tertiary relic, *Dentaria sibirica* (Schultz) Lippmaa.

6. *Hepatica triloba* Gilib. has two wholly isolated areas, the greater one in Central Europe from southern Scandinavia to the Balkans, the other one in eastern Asia. According to Palibin (1898), Komarow (1901) and Nakai (1909), the eastern Asiatic plants are identical taxonomically with the European ones. The old genus *Hepatica* contains only a few species: *H. transsilvanica* Fuss (Hungary, Roumania), the Himalayan *H. Falconeri* (Thomson), the Chinese *H. Henryi* (Oliver) and the American *Hepatica americana* (DC.) Ker. and *H. acutiloba* (DC.) Lawson. This singular distribution of species proves the considerable age of the genus.

7. *Lamium galeobdolon* (L.) Crantz is a European species ranging from England to the Volga river. The subgenus *Galeobdolon* has only four species. Two of them are Mediterranean (*L. pubescens* Sibth. and *L. flexuosum* Tenore) and one occurs in China (*L. chinense* Benth.). The genus is undoubtedly Tertiary.

8. *Lathraea squamaria* L. is a European species with an isolated area in the Himalayas. All the species of this genus [apart from *L. squamaria* L. only *L. clandestiana* L. (southern Europe), *L. rhodopea* Dingler (Balkans), *L. purpurea* Cummins (Himalaya), *L. Nakaharai* Makino (Japan)] existed according to Engler (1879) already in the Tertiary.

9. *Mercurialis perennis* L. is a European species. The range of the *genus* is bicentric, the centers being isolated by an enormous interval. In Europe, apart from *M. perennis* L., the related species *M. ovata* Sternb. and Hoppe and in southern Europe *M. Reverchoni* Roy (Gibraltar), *M. elliptica* Lam., *M. corsica* Coss., *M. pinnatifida* Sennen (Spain), *M. annua* L. (Europe and northern Africa) occur. The other species are eastern Asiatic (*M. leiocarpa* S. et Z., *M. transmorrisonensis* Hayata and *M. acanthocarpa* Leveille et Vaniot). According to Pax, *M. perennis* and *M. ovata* survived the glacial period even in central Europe.

10. *Orobus vernus* L. is a Eurosiberian species. The genus *Orobus* (about 30 species) occurs with many species in southern Europe and the Caucasus. Some species reach far into Siberia (e.g. *Orobus luteus* L.). Eastern Asia

has few species: *O. alatus* Maxim. (related to *O. vernus* L.), *O. humilis* Ser. *O. alpestris* W. et K. occurs in Pontic Europe and after a great interval in Siberia.

11. *Pulmonaria officinalis* L. is a European species which occurs from eastern France to the Kama river. The genus contains 10-12 interrelated species. According to Gams, they are all descendants of the following four Tertiary species: *Pulmonaria officinalis* L., *P. montana* Lejeune, *P. rubra* Schott, *P. angustifolia* L. Their ranges lie in Europe; only *P. montana* extends eastwards to Yakutsk.

12. *Sanicula europaea* L., a European species, occurs also in the Caucasus, on two wholly isolated stations in the southern Ural (Gov. Perm and Ufa), and in the Kuznetski Alatau mountains. In Asia and Africa *Sanicula europaea* L. s. str. is replaced by related species, i.e., in eastern Asia *S. elata* Hamilt. and *S. rubrifolia* F. Schmidt. The genus has numerous species in China, North America, etc. The South African *S. capensis* Eckl. et Z. is, according to Komarow, nearer to *S. elata* Hamilt. (eastern Asia) than to *S. europaea* L. s. str. Undoubtedly, the genus *Sanicula* is very old. Today *S. europaea* L. stands wholly isolated in the European flora.

13. *Stellaria holostea* L. is a European species ranging from England to the Urals and from southern Finland to northern Africa. There are isolated stations in Siberia: Tomsk (Krylow), Tobolsk (Gordjagin).

14. *Viola mirabilis* L. is a Eurasiatic species belonging to the subsection *Rostratae* Kupffer. Related species are *V. Willkommii* De Roem. (Spain) and *V. pseudomirabilis* Coste (endemic species of two isolated stations in southern France and Yugoslavia). The subsection is represented also in China (*V. Stewardiana* W. Bekr.), Japan (*V. labradorica* Schrk.) and North America (*V. adunca* Sm. and *V. labradorica* Schrk.)

The results of the investigation of the relationship of the characteristic species of the *Galeobdolon-Asperula-Asarum* union of Europe may be summarized as follows:

All characteristic species of the union are ancient woodland plants. They often occupy an isolated systematic position. Their relatives occur in the Balkans, the Himalayas, Eastern Asia, North America, countries which are particularly rich in Tertiary relicts. Several of them occur in small and entirely isolated areas in Siberia *(Asperula odorata, Actaea spicata, Sanicula europaea, Stellaria holostea, Asarum europaeum, Bromus Beneckenii, Carex digitata)*. The species of the *Galeobdolon-Asperula-Asarum* union thus existed in the Tertiary.

The Tertiary vegetation of Europe and Asia has been treated by Heer (1878), Engler (1879), Palibin (1904, 1906) and many other authors. Recently Kryshtofovich (1930), summarizing the knowledge of the numerous stations of Tertiary plant remains from the Polish border to the Pacific Islands, concluded:

During the Tertiary the vegetation of Europe differed considerably from

that of Eurasia (in a limited sense). The most important vegetational boundary passed in a NW-SE direction and separated the evergreen subtropical and tropical vegetation of Western Europe and the Ukraine (representatives of the genera *Oreodaphne, Ficus, Cassia, Anona, Sapindus, Cinnamomum,* etc. together with *Nipa* and *Sabel*) from the temperate Arcto-tertiary vegetation of northeastern Europe and Siberia.

The Arcto-tertiary vegetation extended then from North America and Greenland to the Urals and Siberia. In the northern Urals (61° 10′) Kryshtofovich found the following species: *Sequoia Sternbergii* Heer, *S. Langsdorfii* Heer, *Ficus uralisa* Krysht., *Populus Richardsonii* Heer, *Magnolia Inglefieldii* Heer, *Ilex longifolia* Heer, *Macclintockia trinervis* Heer, *M. Lyellii* Heer Urticac.). According to Engler and Kryshtofovich, the Arcto-tertiary vegetation was relatively uniform over extended areas and was composed of diverse, mostly deciduous, species of the folloiwng genera: *Fagus, Castanea, Ulmus, Alnus, Betula, Corylus, Populus, Juglans, Carpinus, Liquidambar, Sequoia, Ginkgo, Quercus, Zelkowa,* etc. Kryshtofovich says this vegetation required an annual temperature average of $+10°C$.

The *Galobdolon-Asperula-Asarum* union undoubtedly existed in the Tertiary. It is admirably adapated to an upper stratum formed by deciduous trees because it needs: (1) light in the spring during the period of flowering, (2) shade in the summer, and (3) a mild humus formed in the woods by deciduous trees.

This suggests the conclusion that the ancient mesophanerophytic union in whose shade the *Galeobdolon-Asperula-Asarum* union has developed was the above mentioned tree layer formed by *Fagus, Ulmus, Alnus, Betula, Juglans, Carpinus, Liquidambar, Ginkgo, Corylus,* and other species. These rich phanerophytic unions have maintained themselves well in North America, eastern Asia and partly also in Europe (especially in the Balkans and the Caucasus).

However, this mesophanerophytic vegetation was completely destroyed in Greenland and nearly so in Siberia by the great glaciation (Fig. 5). In Siberia the glaciation was not as complete as in northern Europe. This explains the possibility that in the Kuznetski Alatau mountains *Tilia cordata* Mill. occurs as a relic and, in its shade, the *Galeobdolon-Asperula-Asarum* union in its special Altaian facies.

The great glaciation brought about a profound change in the vegetation of Europe. The tropic and subtropic vegetation disappeared entirely whereas the temperate vegetation was driven back to southern Europe. Lämmermayr attempted to determine the area occupied by the European and Caucasian beech during the period of maximal glaciation (the dotted areas in Fig. 5).

These beech forests were of special importance for the preservation of the *Galeobdolon-Asperula-Asarum* union during the glacial period. It is not improbable that the union lost many species by its retreat. But it certainly suffered much less than the phanerophytic union. Besides it is very probable that north of the beech forest in the glacial drift there occurred forests and shrubs of other species such as lime-tree, hazel, etc. which served also as a habitat for the *Galeobdolon-Asperula-Asarum* union.

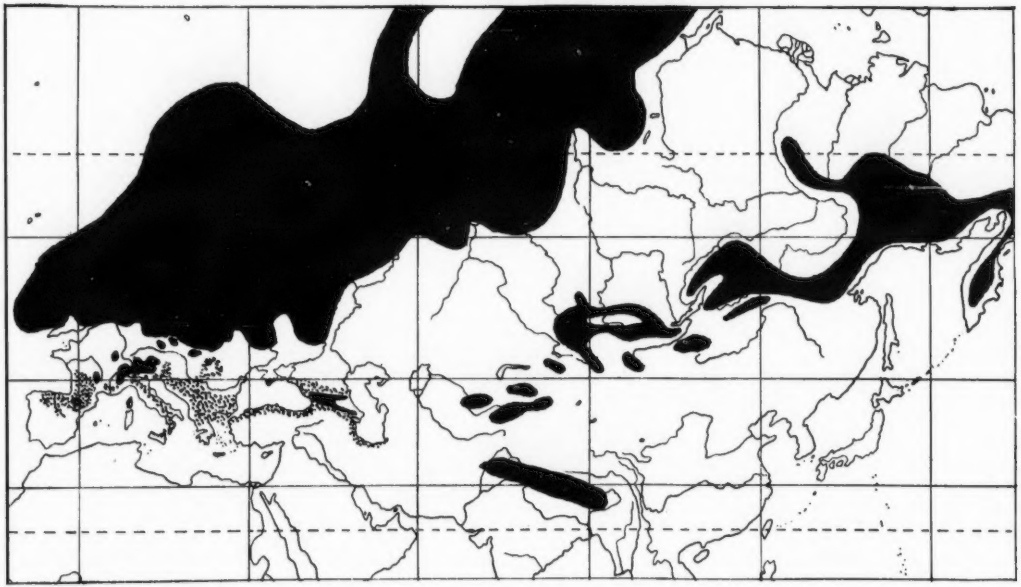


Fig. 5. The maximum of the ice-cover in Eurasia during the glacial drift (after De Geer, Grabmann, Sobolew, Bubnoff, Obrutschew, Tolmatschew, et al.). The dotted areas are the beech-refugiums (after Lämmermayr).

As soon as the climate in the alluvium became better and the glaciers began to retreat in a northern direction or to the mountains the union began to extend its territory. This expansion took place in a general northward direction. Thus many species have gradually reached the present limits of the union whereas others remained behind owing to their less effective means of dispersal. Consequently the present ranges of the species of the union are caused by other factors in addition to climate, soil, and competition. It is interesting to note that the species of the union in question are dispersed by animals. Synzoic dispersal by ants is very common: *Anemone nemorosa, Asarum europaeum, Carex digitata, Dentaria bulbifera, Hepatica triloba, Lamium galeobdolon, Lathraea squamaria, Melica nutans, Pulmonaria officinalis, Viola mirabilis* etc. (Sernander 1901). *Asperula odorata, Mercurialis perennis, Sanicula europaea, Geum urbanum* are dispersed epizoically. Species with endozoic dispersal are *Actaea spicata, Paris quadrifolia, Fragaria vesca, Majanthemum bifolium.*

The *Galeobdolon-Asperula-Asarum* union originates from the Tertiary deciduous forest. Today the protecting tree layer may be very different in different countries. The union occurs in (1) *Fagus silvatica* and (2) *Fagus orientalis* forests, in (3) *Carpinus betulus* forests, in mixed forests formed by (4) *Ulmus montana, Tilia cordata, Acer platanoides* (sometimes mixed with *Picea excelsa*), in (5) the *Tilia cordata* forests of eastern Russia, in (6) the mixed forests of the Ural *(Picea excelsa, Picea obovata, Abies sibirica, Pinus cembra* ssp. *sibirica, Larix sibirica, Populus tremula)*, etc., the protecting tree layer thus being very different.

Following this discussion on the origin of the *Galeobdolon-Asperula-Asarum* union we return to the facies of the union (cf. p. 124).

Not less than eleven facies occur in the territory from England to the Volga river and from southern Finland to the Balkans. An isolated group is formed by the Pontic, Tauric and Kolchic facies. The existence of so many facies is caused by the fact, that not even *two* species have the same range.

The polymorphic character is increased still more by the ability of many species to occur as dominants. Therefore a great number of variants is possible.

The most important variants are the following:

1. *Aegopodium podagraria* var.
2. *Allium ursinum* var.
3. *Asperula odorata* var.
4. *Athyrium-Dryopteris* var.
5. *Carex pilosa* var.
6. *Dentaria-Erythronium* var.
7. *Dentaria quinquefolia* var.
8. *Dryopteris Robertiana* var.
9. *Ficaria verna* var.
10. *Geranium robertianum* var.
11. *Hepatica triloba* var.
12. *Impatiens noli tangere* var.
13. *Lamium galeobdolon* var.
14. *Melica uniflora* var.
15. *Mercurialis perennis* var.
16. *Milium effusum* var.
17. *Orobus aureus* var.
18. *Oxalis-Dentaria bulbifera* var.
19. *Primula acaulis rosea* var.
20. *Sanicula europaea* var.
21. *Scilla bifolia* var.
22. *Trachystemon orientale* var.

Their distribution in the different facies still needs study. At present

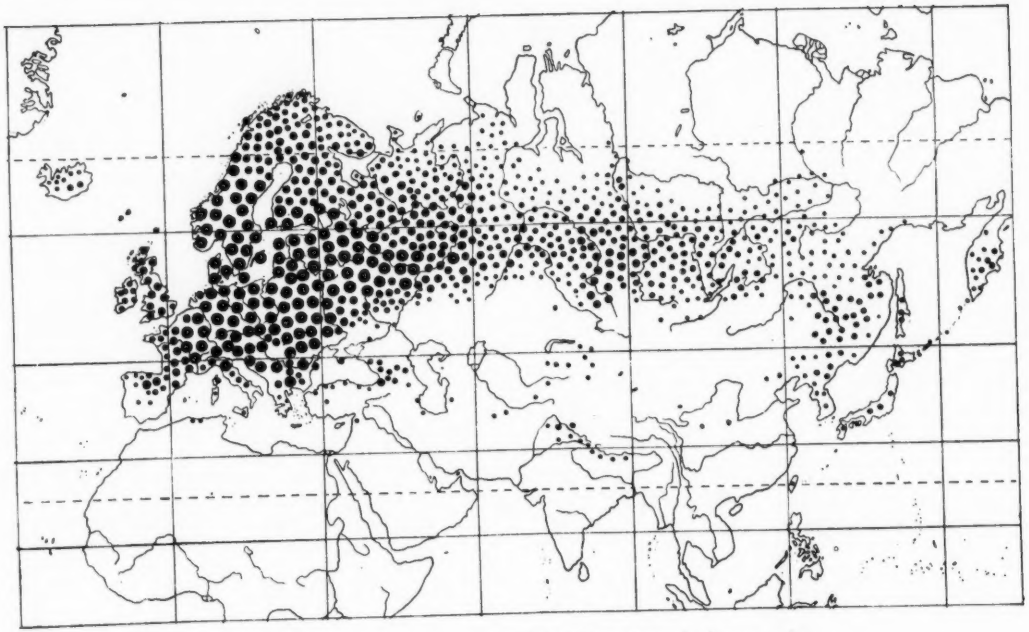


Fig. 6. Distribution of constants of the Galeobdolon-Asperula-Asarum union.

only variants 2 and 20 are mentioned for the Atlantic facies; for the central European facies variants 2-5, 8-16 are known. Obviously, the name of a variant must be given with the name of the facies, because a variant has characteristic differences in its floristic composition conditioned by its membership in a facies. For instance, the *Asperula odorata* variant of the Atlantic facies shows typical and constant differences if compared, e.g., with the *Asperula odorata* variant of the Balto-cassubian facies, or that of the Sarmatic facies.

Only after careful researches throughout its whole range can a union be finally circumscribed and the facies with their variants distinguished. Local investigations ordinarily deal with variants of unions as yet unknown. Therefore, a term is needed for these "unsettled" variants to make possible further local studies, and to serve as a basis for further synthetical researches. It seems best to call them *"societies"* (cf. Du Rietz 1936).

Thus the terminology for one-layered communities reads as follows:

Du Rietz et Gams 1935	Lipmaa 1938
society	variant (society)
	facies
union	union

The one-layered method is based upon the study of societies which are really variants of some facies of certain unions. In the recognition of societies the fundamental differences between patches (sometimes extensive) and stands should be considered.

The question of the relative significance of "characteristic species" and "constants" in the recognition and characterization of a community has been repeatedly the object of discussion. As shown previously, it was possible to determine the range of the *Galeobdolon-Asperula-Asarum* union starting from the characteristic species of this union.

Using the same method as previously (p. 122), the synthetic map showing the distribution of the constants of the *Galeobdolon-Asperula-Asarum* union was prepared (Fig. 6). A comparison of Fig. 3 and Fig. 6 suggests the following conclusions:

(1) The range of the bulk of the constants is much greater than the range of the bulk of the characteristic species, especially northward and eastward. Whereas the northern boundary of the range passed the polar circle in Scandinavia, the southern boundary remains unchanged or nearly so.

(2) *The range of the constants is not identical with the range of the union.* The accumulation of constants in northern Scandinavia is occasioned by species such as *Viola mirabilis, Milium effusum, Majanthemum bifolium, Fragaria vesca, Rubus saxatilis, Oxalis acetosella, Paris quadrifolia, Trientalis europaea* which very often occur in the *Galeobdolon-Asperula-Asarum* union (in the Balto-cassubian facies they are constant) but their true place is not in this union.

It seems to the author that this result is a warning not to overestimate the importance of constants. The key to the nature of a community is given by its characteristic combination of species in the broader sense and by the habitat.

For the study of a society a knowledge of the habitat is of eminent importance. In the first part of this paper (p. 113) the analysis of the floristic composition and some other phytosociological characters of the *societies* of the *Nobilifrondetum herbosum* in Estonia were given. This analysis was carried out essentially in the lime-tree forest of the island of Abruka (Lippmaa, 1935). To complete these researches, investigations concerning the habitat were carried out during the summer of 1937.

The author is as yet unable to characterize completely the habitat of each society of the community. Although further researches are indispensable, some general features seem to be clear.

Temperature. The average annual temperature on the adjacent peninsula of Sorve is as follows:

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Year
–2.5	–3.3	–1.9	2.4	7.7	13.1	16.4	15.6	12.7	7.7	3.1	–0.3	5.9

To ascertain the daily temperature changes in the habitats of the diverse societies, minute determinations of the air temperature were carried out in the different layers. These measurements were made by two thermographs (Fuess, Berlin) during the whole summer. The results obtained may be summarized as follows:

Above the *Ulmus-Acer-Tilia* society at a height of 33 m. from the soil, the vegetation is exposed to the direct sunlight. Wind and sun together cause a characteristic finely denticulated curve. During fine weather in June, July and August the daily changes of temperature are from 15°C. to 25°C. (29°C.).

The *Corylus avellana* society (about 4-6 m from the soil surface) has less amplitude. The curve here is more regular. Only here and there the temperature rises suddenly from 3° to 5° C. for a quarter of an hour caused by the direct light passing. This character of the temperature curve also applies to the *Lonicera xylosteum-Ribes alpinum* society, the variants of the *Galeobdolon-Asperula-Asarum* union and the *Rhytidiadelphus triquetrus-Eurhynchium striatum* society. The daily changes of temperature during fine weather are from 14° C. to 22° C. (25°C.) in the *Lonicera xylosteum-Ribes alpinum* society and also in the *Asperula odorata* variant of the *Galeobdolon-Asperula-Asarum* union, but from 15° C. to 25° C. (28° C.) in the *Rhytidiadelphus triquetrus-Eurhynchium striatum* union.

It is noticeable, that in all habitats between 0 and 6 m. above the ground the thermographs registered in August many more "sun flecks" than in June and the first half of July. The very characteristic denticulate curve mentioned above appears there, although never as pronounced as in the *Ulmus-Acer-Tilia* community.

As may be seen from Fig. 7, the habitat of the *Ulmus-Acer-Tilia* society differs in its temperature conditions from the protected *Corylus avellana*

society and the other societies of the lower layers. The differences between the societies protected by the tree-layer are scarcely perceptible.

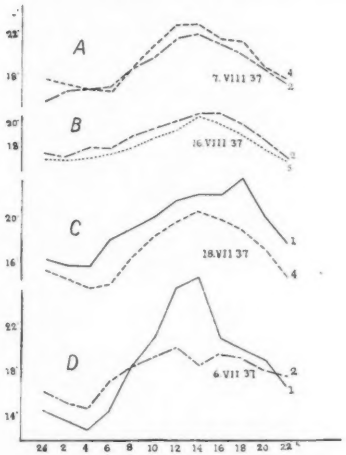


Fig. 7. The range of daily temperature in Ulmus-Acer-Tilia society (1), Corylus avellana soc. (2), Asperula odorata soc. (4), and Rhytidiadelphus-Eurhynchium society.

Light. The intensity of light in each habitat was measured by the Lange photoelement. The measurements are very easy to carry out and were taken separately for conditions of diffuse and direct light. There are in a forest all transitions from patches of direct light to deep shade. To obtain more or less satisfactory results the number of individual measurements must be at least 5 to 10 in each case. Fig. 8 represents some of the results thus obtained. The light intensity is greatly reduced by the *Ulmus-Acer-Tilia* society. The

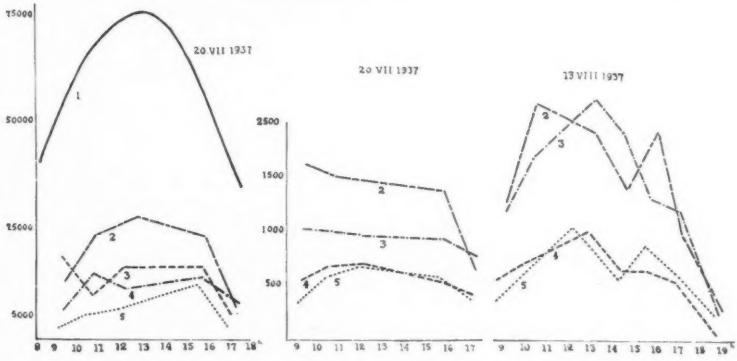


Fig. 8. The range of the light density in Ulmus-Acer-Tilia soc. (1), Corylus soc. (2), Lonicera-Ribes soc. (3), Asperula odorata soc. (4), and Rhytidiadelphus-Eurhynchium soc. (5).

difference between the light condition of this society and the *Corylus avellana* society therefore is very great. For instance on July 20th the maxima observed were: 75,000 Lx (*Ulmus-Acer-Tilia* soc.), 25,500 Lx (*Corylus avellana* soc.), 14,500 Lx (*Lonicera xylosteum-Ribes alpinum* soc.), 16,000 Lx (*Asperula odorata* var.), 12,000 Lx (*Rhytidiadelphus triquetrus-Eurhynchium striatum* soc.). These values were obtained in direct light. But direct light lasts only a short time in a given place in a society like *Corylus avellana* and other "*protected societies.*" Therefore, the differences in the light conditions are much greater than may be deduced from the numbers obtained.

The measurements of diffuse light gave on the same day the following maxima: 1,597; 1,009; 685; 634, for societies from the *Corylus avellana* society to the *Rhytidiadelphus triquetrus-Eurhynchium striatum* society. The difference in these values is less than 1:3. When this figure is compared with the light intensity in the assimilating parts of the *Ulmus-Acer-Tilia* society (open light), the intensity is only 1/47 to 1/118.

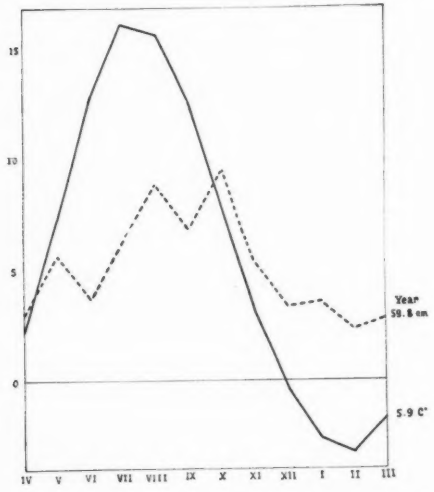


Fig. 9. The range of temperature and precipitation on the Island Abruca (Estonia).

In August the intensity of light in all societies (except *Ulmus-Acer-Tilia* society) *increased* rather than decreased. This phenomenon became especially pronounced at the end of the month. On August 13th the measurements of diffuse light gave the following maxima: 2,250; 2,300; 1,070; 1,117. The increase is about 1:1.5 or 1:2. The maximum light intensity above the *Ulmus-Acer-Tilia* society was 56,000 Lx on this day.

The explanation of this seemingly paradoxical statement will be given later.

Water. Fig. 9 shows the annual course of precipitation on the island. The average precipitation is 625 mm. per year. But it sometimes happens

that the annual amount is only 400-500 mm. The summer is often very dry; the autumn rains begin in August or September. The determination of the *relative humidity* of the air in the habitats was carried out with the Assmann psychrometer. Great differences were found in the first part of the summer (Fig. 10 A, B). There was a distinct increase of humidiity from the *Ulmus-Acer-Tilia* society to the *Rhytidiadelphus triquetrus-Eurhynchium striatum* society.

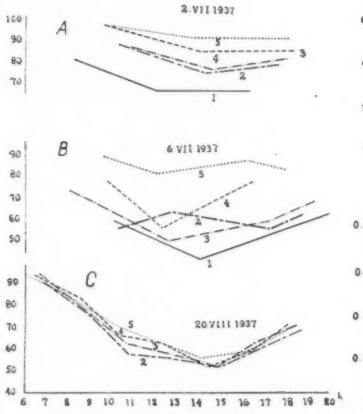


Fig. 10. The daily range of relative air humidity (given in percentages) in Ulmus-Acer-Tilia soc. (1), Corylus soc. (2), Lonicera - Ribes soc. (3), Asperula odorata soc. (4), and Rhytidiadelphus-Eurhynchium soc. (5).

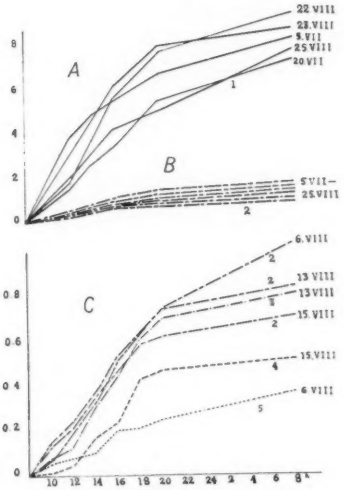


Fig. 11. The rate of evaporation in the societies of the lime tree forests on Abruca. 1-Ulmus-Acer-Tilia Soc., 2-Corylus avellana soc., 3-Lonicera-Ribes soc., 4, Asperula odorata soc., 5-Rhytidiadelphus-Eurhynchium soc.

Since the summer of 1937 was very dry, these differences disappeared gradually and finally the results shown in Fig. 10 C were obtained. The curves for different societies nearly coincide.

For plant life the relative humidity (and the saturation deficit) is of great importance as a factor influencing transpiration. No less important is a knowledge of the evaporation rate, because it results from the combined effects of humidity, wind, and temperature, to mention only the most important factors.

Measurements of the evaporation rate were taken with three Iwanoff phytoatmometers.

The following results were obtained (Fig. 11 A, B). Evaporation in the *Ulmus-Acer-Tilia* society was about 5.5 times more intensive than in the

Corylus avellana society. The differences between *Corylus avellana* society, *Lonicera xylosteum-Ribes alpinum* society, *Asperula odorata* variant and *Rhytidiadelphus triquetrus-Eurhynchium striatum* society were not distinct, at least during the very dry period in August 1937 (cf. Fig. 11 C). Nevertheless the evaporation in the *Corylus avellana* society was found to be greater than in the lower situated societies in the proportion of 13 to 10.

In the second half of July and in August the drought became more and more pronounced. The following table sums up the facts observed.

The effect of drought in a deciduous forest with lime-tree dominating (Island of Abruka, Estonia) in the summer 1937.

Tilia cordata	g·	g·	g·	g·y·	g·y·	g·y·	g·y·	g·y·
Betula verrucosa	g·	g·	g·	g·y·	g·y·	g·y·	g·y·	g·y·
Ulmus montana	g·	g·	g·	g·y·	g·y·	g·y·	g·y·	g·y·
Sorbus aucuparia	g·	g·	g·	g·	g·r·	g·r·	g·r·	g·r·
Quercus robur	g·	g·	g·	g·	g·	g·	g·	g·
Salix caprea	g·	g·	g·	g·	g·	g·	g·	g·
Acer platanoides	g·	g·	g·	g·	g·	g·	g·	g·
Fraximus excelsior	g·	g·	g·	g·	g·	g·	g·	g·
Corylus avellana	g·	g·	g·y·	g·y·	g·y·	g·y·	g·y·	g·y·
Daphne mezereum	t·	t·w·	w·	w·	t·	w·	w·	w·t·
Lonicera xylosteum	t·	t·	t·	t·	t·	t·	t·w·	w·t·
Ribes alpinum	t·	t·	t·	t·	t·	t·	t·w·	w·t·
Aegopodium podagr.	t·	t·	w·	w·	t·	t·	w·	w·t·
Mercurialis perenn.	t·	t·	w·	w·	t·	t·	w·	w·t·
Stachys silvatica	t·	t·	t·w·	w·	t·	w·	w·	w·t·
Asperula odorata	t·	t·	t·	t·	t·	t·	t·w·	w·t·
Orobus vernus	t·	t·	t·	t·	t·	t·	t·w·	w·t·
Carex digitata	t·	t·	t·	t·	t·	t·	t·	w·t·
Fragaria vesca	t·	t·	t·	t·	t·	t·	t·	w·t·
Hepatica triloba	t·	t·	t·	t·	t·	t·	t·	w·t·
Oxalis acetosella	t·	t·	t·	t·	t·	t·	t·	t·
Majanthemum bifol.	t·	t·	t·	t·	t·	t·	t·	t·
Convallaria maj.	t·	t·	t·	t·	t·	t·	t·	t·

g—green and turgescent leaves, y—yellow and turgescent leaves, r—reddish colored turgescent leaves, t—turgescent, w—withered green leaves.

All four societies reacted more or less simultaneously to the drought but not in the same way. Two distinct groups may be distinguished. To the first group belonged the *Ulmus-Acer-Tilia* society and the *Corylus avellana* society. Withered foliage was observed, though only in exceptional cases (Corylus). The drought caused here a premature formation of yellow and red autumnal foliage which began to drop. In August the ground in the forest was almost a brownish carpet of dead leaves. At the end of August less than half of the summer foliage remained on the dominating species, the lime tree.

This change caused the increase of light intensity in the lower layers (p. 134) during the second part of the summer.

To the second group belonged the *Lonicera xylosteum-Ribes alpinum* society and the *Asperula odorata* variant. There was scarcely any autumnal foliage produced. Only when the dryness became too great for *Daphne mezereum* did the leaves drop whereas others merely withered. After rain they soon became turgescent.

Determinations of water content (in percentage of dry weight) in some species of the *Galeobdolon-Asperula-Asarum* union during the summer gave the following results:

	July 7	July 22	August 6	August 22
Asperula odorata	609	463	495	242
Orobus vernus	397	337	373	187
Mercurialis perenn.	455	392	440	369
Hepatica triloba	361	358	357	292
Carex digitata	282	235	255	215
Oxalis acetosella	680	622	698	616

During the drought the majority of species had closed stomata even during daytime (proved by the infiltration method using alcohol and xylol).

It is rather surprising, that the luxuriant vegetation of a lime-tree forest occurs in habitats where the water factor is occasionally below the necessary minimum. The dominant forest association of Estonia is the mixed forest of deciduous and coniferous trees with *Picea excelsa* dominant. The pure large-leaved deciduous forest (with the *Ulmus-Acer-Tilia* society in the upper stratum) is rare occurring more often only in western Estonia, especially on the islands, and in continental Estonia on well drained slopes.

The question arises: what is the cause, that in these localities *Picea* cannot compete as successfully with the deciduous species as elsewhere in Estonia? This was supposed to be due to the more maritime climate of western Estonia, but now it seems that the true causes are the edaphic conditions and the fact that drought resistance of the Estonian forest trees increases in the following series:

$$\text{Picea} < \begin{matrix}\text{Tilia, Ulmus,}\\ \text{Sorbus Betula}\end{matrix} < \begin{matrix}\text{Quercus}\\ \text{Acer}\end{matrix} < \text{Pinus}$$

Picea occurs abundantly on the island, but only in relatively moist or wet places and then often with *Alnus glutinosa* and *Betula pubescens*. From these places it penetrates by seeds into the adjacent lime-tree forest during every seed year. Yet in the analysis of moss and herb layers *Picea* seedlings are never found. Nevertheless very scattered individuals of *Picea excelsa* occur some of which were examined. They are small trees (5-6 m high) with densely placed branches. The diameter of stems at a height of 20 cm. from the ground was 9-10 cm., the age from 52 to 66 years. Thus in the areas on the island occupied by the lime-tree forest, the spruce is unable to enter into competition with the lime-tree, elm and other deciduous trees.

Edaphic factors. The island of Abruka is relatively young being about 2,000-3,000 years old. It has risen from the sea by the secular elevation of

land and is still growing year by year. Only the oldest, that is the highest part of it, is occupied by the *Nobilifrondetum*. The subsoil is a coarse gravel mixed with stones, fine gravel and sand. The uppermost layer of soil is rich in humus with about 12% of organic matter and without gravel. This layer has a great water capacity. The water content of the different layers of soil is very instructive as may be seen from the following table containing data from five sample plots.

Water content in per cent.

	Mercurialis perennis variant			Asperula odorata variant	
Depth	10 July	12 July	22 August	12 August	13 August
0–12	26.7	30.9	24.5	30.1	19.0
12–25	5.1	12.6	14.9	5.4	5.2
25–55		1.3	1.5	1.1	2.1
55–80	13.2	2.5	1.9	7.9	4.6
80–110		6.2	2.6	32.1	

The chief water reserves are in the uppermost layer rich in humus. Even in the dry summer months there was about 20-30% total water content. The growth water ("chresard") of individual species was not determined. At the end of August in dry weather when a great many of the species of the *Galeobdolon-Asperula-Asarum* union had withered, the total water content of the humus layer was (average of 10 determinations) 16.11 percent in the *Mercurialis perennis* variant and 16.14 in the *Asperula odorata* variant.

The deeper layers of the soil contained water in quantities too low to be accessible to the plants. The third layer with the total water content often only 1-2 percent was extremely dry. Therefore, the water factor is of eminent importance to the vegetation in consideration.

The competition in the uppermost 10-15 cm was extremely sharp. In the following table some data concerning the depth and length of roots on the area investigated are presented.

	The depth at which the roots are found		Maximum length of roots observed
	The chief mass of roots	Single roots	
Tilia cordata	5.10 cm	90 cm	300–500 cm
Acer platanoides	5–7 cm	50 cm	over 1000 cm
Corylus avellana	3–7 cm	30 cm	over 1000 cm
Daphne mezereum	5–7 cm	15 cm	72 cm
Lonicera xylosteum	3–6 cm	20 cm	150 cm
Asperula odorata	1–3 cm	5 cm	
Mercurialis perennis	3–5 cm	8 cm	
Hepatica triloba	3–7 cm	15 cm	
Dentaria bulbifera	3–5 cm	12 cm	
Oxalis acetosella	2–4 cm	8 cm	
Majanthemum bifolium	2–5 cm	10 cm	
Carex digitata	1–5 cm	15 cm	
Milium effusum	1–4 cm	8 cm	
Orobus vernus	3–9 cm	25 cm	
Luzula pilosa	2–5 cm	10 cm	

This uppermost, water-containing layer, rich in humus is the only layer which, in the summer, obtains a water supply by rain. The humus is of a brownish color with well developed crumb structure, with numerous earthworms and with the properties of mull. Yet its pH was relatively low 5.3 to 6.3, ordinarily 5.5. With increasing depth the soil becomes less acid, because gravel and stones are largely composed of limestone.

In a profile under the *Mercurialis perennis* variant the following percentage of $CaC0_3$ was observed:

Depth:	10–12	12–25	25–55	55–80	80–110
$CaC0_3$ %:	0.13	0.04	2.73	2.83	13.98

The trees doubtless keep large amounts of calcium from the deeper soil layers as may be seen in the mature leaves of *Tilia cordata* which are full of calcium oxalate glands. The dead leaves therefore furnish new calcium for the uppermost soil layer.

The capacity of the soil for nitrification could not be determined. It seems, however, that nitrification is efficient judging from the luxuriant vegetation.

The aëration of the soil is satisfactory. Determinations of air capacity by the Kopecky-Siegrist method partly modified by the author gave the following results (under different sample plots of the *Mercurialis perennis* variant):

Analysis:	1	2	3
Air capacity in volume per cent.	7.4	6.0	10.6
Water capacity in volume per cent.	55.7	60.2	63.1
Soil particles and roots in vol. per cent.	36.9	33.8	26.3

Some remarks regarding the moss and lichen societies must still be made.

The *Rhytidiadelphus triquetrus-Eurhynchium striatum* society occurred only in small scattered patches on more or less elevated points (stones, dead branches of trees, etc.) on the ground. Since in mixed forests with *Picea* dominant the ground was often covered by a continuous carpet of this society, the cause of this striking behavior presented a problem.

The study of light conditions, of the pH of the soil surface and of many other factors of the habitat occupied by the mosses and in other places where the mosses were lacking, brought no solution. The explanation was found in the abundant cover of dead leaves which is renewed each year and which is so characteristic of the deciduous forest.

In the *Nobilifrondetum herbosum* many societies of epiphytic lichens and mosses were luxuriantly developed (p. 113). The ecology of these societies needs special investigation. It would be interesting to determine their chief period of vegetative life. It seems to the author, that the months of August, September and October (and perhaps the spring) are very favorable for them: (1) the foliage is much less dense and at last disappears completely; (2) the autumn rains and mists may favor the assimilation of epiphytic mosses and lichens.

The preceding discussion emphasized the diversity of societies existing in a single association. Each of them has not only a certain floristic composition

but also a characteristic habitat. They are undoubtedly well developed communities.

As shown previously, each society is really a variant of a facies of a community called a union. The *Galeobdolon-Asperula-Asarum* union is not the only union of the large-leaved deciduous forest. Ecologically closely related unions occur in eastern Asia and in North America. In eastern Asia (Manchuria) it is the *Caulophyllum-Pilea viridissima* union (cf. Lippmaa 1938 p. 141), in America the *Viola-Arisaema* union described by Cain (1934). The important elementary life-form Lippmaa 1933) in all three is the *Anemone* life-form (*Anemone, Podophyllum, Trillium, Dentaria, Panax*, and other species).

How are unions to be classified? The author agrees with Warming, Rübel, Nichols et al. that the classification of plant communities without doubt must be ecological.

A concrete example is given in the author's treatise of 1933 (p. 112-118) where a classification of the vegetation of Estonia is attempted on the basis of the societies (= one-layered associations) present and their habitats. This method may be applied without principal difficulties to include the vegetation of the earth.

The unions mentioned above could be classified as follows:

Dominating life-form ↓	Habitat ——→	
Unions of hemicryptophytes and cryptophytes	Temperate zone	
	1. Habitats of Sciophytes in Lignosa	2. . . . .
	1. Aestilignosa 2. . . .	
	1. Hab. with well developed mull	
1. Unions with frequent occurrence of the Anemone life-form	1. Galeobdolon-Asperula-Asarum un. (Euras.)	
	2. Arisaema-Viola un. (Atl. North Am.)	
	3. Caulophyllum-Pilea un. (Manchur.)	
	4. ----------	
	5. ----------	

Warming, Flahault, and others classified communities simultaneously on the basis of 1) the dominant life-forms and 2) the haabitat. But this method is impracticable as long as phytosociological studies are based upon several-layered and therefore upon heterogeneous associations.

REFERENCES

BRAUN-BLANQUET, J. AND J. PAVILLARD. 1928—Vocabulaire de Sociologie Végétale 3 ed. Montpellier.

———1932—Zur Kenntnis nordschweizerischer Waldgesellschaften. Station Intern. de Géobot. Medit. et Alp. Montpellier Communication **17**.

———1932—Plant Sociology. Translated by G. D. Fuller and H. S. Conard.

CAIN, STANLEY A. 1934—Studies on Virgin Hardwood Forest: II. A comparison of quadrat sizes in a quantitative phytosociological study of Nash's Woods, Posey County, Indiana. Amer. Midl. Natur. **15**(5):529-566.

———1935—Ecological studies of the vegetation of the Great Smoky Mountains. Amer. Midl. Natur. **16**(4):566-584.

———1936—Synusiae as a basis in plant sociological field work. Amer. Midl. Natur. **17**(3):665-672.

———AND W. M. T. PENFOUND. 1938—Aceretum rubri: the red maple swamp forest of central Long Island. Amer. Midl. Natur. **19**(2):390-416.

CAJANDER, A. G. 1922—Zur Begriffsbestimmung im Gebiet der Pflanzentopographie. Acta Forest. Fenn. **20**, Helsinki.

CLEMENTS, FREDERIC E. 1936—Nature and Structure of the Climax. Jour. Ecol. **24**(1).

CONARD, HENRY S. 1935—The Plant Associations of Central Long Island. Amer. Midl. Natur. **16**(4):433-516.

DOMIN, K. 1932—The Beech Forest of Czechoslavakia. Veröff. d. Geobot. Inst. Rübel in Zürich **8**.

DURIETZ, G. EINAR. 1921—Zur methodologischen Grundlage der modernen Pflanzensoziologie. Akad. Abhandlung. Upsala.

———1930—Classification and nomenclature of vegetation. Svensk Bot. Tidskr. **24**(4).

———1930—Vegetationsforschungen auf soziationsanalytischer Grundlage. Handbuch d. biol. Arbeitsmethod. Abt. 11, T. 5. Berlin und Wien.

ENGLER, AD. 1879—Versuch einer Entwicklungsgeschichte der Pflanzenwelt.

FLEROFF, A. F. 1899—Oc. rastit. sewerozapadn. casti Vladimirsk. Gub.

FLAHAULT, CH. UND C. SCHRÖTER. 1910—Phytogeographische Nomenclatur. Zürich.

GAMS, H. 1918—Prinzipienfragen der Vegetationsforschung. Vierteljahrschr. d. Naturf. Gesellsch. in Zürich **43**.

———1927—Von den Follateres zur Dent de Morcles. Vegetationsmonographie aus dem Wallis. Beiträge zur geobot. Landesaufnahme **15**.

GANESCHINE, S. S. 1927—Forêts aux caractères primitifs dans quelques regions du district de Louga. Leningrad.

HÄYREN, E. 1914—Über d. Landvegetation und Flora d. Meeresfelsen von Tvärminne. Acta Soc. pro Fauna et Flora Fennica **39**. Helsingfors.

HEER, O. 1879—Fossile Pflanzen von Sumatra. Denkschr. d. schweiz. naturf. Gesellsch.

HRYNIEWIECKI, B. 1933—Tentamen Florae Lithuaniae. Arch. Biol. Soc. Sci. et Lett. Varsovie **4**.

KOCH, W. 1926—Die Vegetationseinheiten der Linthebene unter Berücksichtigung der Verhältnisse in der Nord-ostschweiz.

KLIKA, J. 1928—Une étude géobotanique sur la végétation de Velka Hora près de Kalstejn. Bull. Internat. de l'Acad. Sci. de Boheme.

———1932—Lesy v xerothermni oblasti Cech. Wälder im xerothermen Gebiete Böhmens (Ein Beitrag zur Typologie der Wälder in CSR. Eine soziologische Studie).

KOTILAINEN, M. J. 1928—Untersuchungen über die Beziehungen zwischen der Pflanzendecke der Moore und der Beschaffenheit, besonders der Reaktion des Torfbodens. Suomen Soviljelysyhdist. Tieteellisiä Julkaisuja **7**. Helsinki.

KORSHINSKY, S. 1888—Bot.-geogr. otscherk Kasansk. gub.

KRYSHTOFOVICH, A. 1930—Principal features of evolution of the Tertiary Flora in Asia. Bull. Jard. Bot. Princip. de l' URSS.

KUJALA, V. 1925—Über die Begrenzung der Siedelungen. Commun. ex Inst. quaest. forestal. Finlandiae editae **10**. Helsinki.

———1929—Die Bestände und die ökologischen Horizontalschichten der Vegetation. Acta Forest. Fennica **34**. Helsinki.

———1936—Waldvegetationsstudien im östlichen Mitteleuropa. Commun. Inst. Forest. Fenniae **22**(6).

KUPFFER, K. R. 1931—Die Naturschonstätte Moritzholm. Arbeit Naturforscher- Ver. Riga, N. F. **19**.

LINDQUIST, B. 1932—The Beech Forest of Sweden. Veröff. d. geobot. Inst. Rübel in Zürich **8**.

LIPPMAA, T. 1926—Pflanzenökologische Untersuchungen aus Norwegisch- und-Finnisch-Lappland unter besonderer Berücksichtigung der Lichtfrage. Acta Inst. et Horti Botan. Univ. Tartuensis **2**.

———1931—Pflanzensoziologische Betrachtungen. Sitzungsb. d. Naturforsch. Gesellsch. Univer. Tartu **38**(1-2).

———1932—Beiträge zur Kenntnis der Flora und Vegetation Südwest-Estlands. Acta Inst. et Horti Botan. Univ. Tartuensis **2**(3-4); Esti Loodusteaduse arhiiv (Archiv für die Naturkunde Estlands) II Ser., **13**(3).

———1933—Aperçu général sur la végétation autochtone du Lautaret (Hautes Alpes) avec remarques critiques sur quelques notions phytosociologiques. Acta Inst. et Horti Bot. Univ. Tartuensis **3**.

———1933—Taimeühingute uurimise metoodika ja Eesti taimeühingute klassifikatsiooni põhijooni. (Referat: Grundzüge der pflanzensoziologischen Methodik nebst einer Klassifikation der Pflanzenassoziationen Estlands, pp. 140-159). Acta Inst. et Horti Botan. Univ. Tartuensis (Dorpatensis) **3**(3):1-169.

———1934—La méthode des association unistrates et le système écologique des associations. Tartu Ülikooli juures oleva Loodusuur. Seltsi Aruand. **41**(3,4).

———1935—Une analyse des forêts de l'île estonienne d'Abruka (Abro) sur la base des associations unistrates. Acta Inst. et Horti Botan. Univ. Tartuensis **4**(1, 2).

———1935—Eesti geobotaanika põhijooni, Aperçu géobotanique de l' Estonie. Acta Inst. et Horti Botan. Univ. Tartuensis **4**(3-4).

———1938—Areal und Altersbestimmung einer Union (Galeobdolon-Asperula-Asarum-U.) sowie das Problem der Charakterarten und der Konstanten. Acta Inst. et Horti Botan. Univ. Tartuensis **6**(2):1-152.

LUNDEGARDH, H. 1925—Klima und Boden in ihrer Wirkung auf das Pflanzenleben. Jena.

LÄMMERMAYR, L. 1923—Die Entwicklung der Buchenassoziation seit dem Tertiär. Rep. spec. nov. regn. veget. Beih. **24**.

MARKGRAF, FR. 1932—Der deutsche Buchenwald. Veröff. d. geobot. Inst. Rübel **8**.

MEUSEL, H. 1935—Die Waldtypen des Grabfeldes und ihre Stellung innerhalb der Wälder zwischen Main und Werra. Beih. Bot. Cbl. Abt. B, **53**(1).

NORDHAGEN, R. 1928—Die Vegetation und Flora des Sylenegebietes. I. Die Vegetation. Skrift. Norske Videnskaps-Akad. Oslo 1927, I: Mat.-Naturvid. Kl. **1**.

OSTENFELD, C. H. 1932—The Danish Beech-forests. Veröff. d. geobot. Inst. Rübel in Zürich **8**.

PACZOSKI, J. 1929—Lasy Bosni (Die Wälder Bosniens). Odbitka z "Sylwana" organu Polskiego Tow. Lesnego. Rocznik XLVII. Zeszyt 5.

———1930—Social Life of Plants. Biblioteca Botaniczka **2**, Krakow.

PALIBIN, J. B. 1906—Iskopaem. rasten. bereg. Aralskogo morja. Izw. Turkest. Otd. Imp. Ross. Geol. Ob. **4**.

PALMGREN, A. 1922—Über Artenzahl und Areal sowie über die Konstitution der Vegetation. Acta Forest. Fennica **22**.

PAVILLARD, J. 1935—Élements de sociologie végétale (Phytosociologie). Paris.

REGEL, C. 1923-1928—Die Pflanzendecke der Halbinsel Kola. Lietuvos Univ. Matem. —Gamtos Fakult. Darlu, Kaunas.

———1923—Litauen and Rumänien. Ein Vergleich. Veröff. d. geobot. Inst. Rübel in Zürich **10**.

———1927—Zur Klassifikation der Assoziationen der Sandböden. Englers Bot. Jahrb. **61**.

RÜBEL, E. 1930—Pflanzengesellschaften der Erde. Bern-Berlin.

SERNANDER, R. 1925—Exkursionsführer für Skåne. 4. Internat. Pflanzengeogr. Exk. (I.P.E.) durch Skandinavien.

SIRKS, M. J. 1936—Proc. Zesde Intern. Botanisch. Congres. **1**.

SOO, R. 1927—Geobotanische Monographie von Kolozsvar (Klausenburg). Mitt. Kom. f. Heimatk. d. Wiss. Gr. Stefan Tisza Ges. Debrecen **4**.

SUKATSCHEW, W. 1929—Über einige Grundbegriffe in der Phytosoziologie. Ber. Deutsch. Bot. Ges. **47**.

SZAFER, W. 1935—Las i step na zachodniem Podolu (The forest and the Steppe in West Podolia). Osobne odbicie z Rozpran Wydzialu matematyczno-przyroduiczego Polskiej Akademji Umiejetnosci, **71**, Dz. B, 2.

TANSLEY, A. G. 1923—Practical Plant Ecology.

TÜXEN, R. 1937—Mitteilungen der floristisch-soziologischen Arbeitsgemeinschaft in Niedersachsen. Beih. Jber. naturhist. Ges. Hannover, **3**.

VIERHAPPER, F. 1932—Die Rotbuchenwälder Oesterreichs. Veröff. d. Geobot. Inst. Rübel in Zürich **8**.

WARMING, E. UND P. GRAEBNER. 1918—Lehrbuch der ökologischen Pflanzengeographie, 3. Aufl., Berlin.

WATT, A. S. AND A. G. TANSLEY. 1932—British Beech Woods. Veröff. d. geobot. Inst. Rübel in Zürich **8**.

DISCUSSION

Tansley: (by cablegram from Grantchester, Cambridge): "Warmest greetings to conference! Stratum best international term for Lippmaa's one-layered association wherever part of many-layered community."

Lippmaa: I should be very glad to agree with this proposal were it not for certain difficulties. The first and most important of these is the fact that the system of unions is not based solely on stratification. For the essential feature is not that the unions are unistratal although this also holds true, but the fact that the bulk of the species of a union belongs to the same life-form. For instance in the northwestern Sahara the society formed by therophytes (known as "Asheb") belongs to a totally different union if compared with the society formed by chamaephytes like *Fredolia aretioides*, *Launaea arborescens*, *Zilla moeroptera*, etc. However during some weeks both occur closely together in the same stratum. Thus two unions may occur in the same stratum, at the same time, and on the same piece of ground.

The term "union" proposed by Du Rietz and Gams for my "unistratal association" is already being used by Cain, Sirgo, Pastak and myself.

Steiger: How would *Rhus toxicodendron*, poison ivy, be treated in such a union when it covers a forest floor?

Lippmaa: My knowledge of the American vegetation is insufficient to pass judgment.

Conard: This remark has reference to lianas which may or may not climb. I believe *Hedera helix* is a European species of that behavior.

Lippmaa: In northern Europe *Hedera helix* belongs to the *Galeobdolon-Asperula-Asarum* union because during the winter the parts not protected by snow are killed. In the tropics the lianas seem to form distinct unions.

Conard: What category higher than the union does this system recognize? Are there alliances and classes of unions?

Lippmaa: I classify unions according to the life forms which predominate in them and according to the condition of habitats. The highest units are *Divisions* (e.g. the division of hemicryptophyte-cryptophyte unions, the division of therophyte unions), the divisions contain many classes (e.g. the class formed by the hemicryptophyte unions of the temperate zones, the hemicryptophyte unions of northern Africa), and the class of unions contains some families and these in turn some genera. There is a genus which contains the related unions Galeobdolon-Asperula-Asarum union (Europe), Caulophyllum-Pilea union (Manchuria), Arisaema-Viola union (Atlantic North America). Their habitat is the deciduous forest of the temperate zone. Alliances and orders based on floristic affinities are not suitable for the classification of unions.

Conard: This brings out the necessity of considering mosses and lichens as a part of the plant community, a thing which we in America almost entirely fail to do. It was in recognition of that precedent that this laboratory undertook to further the publication of Grout's "Moss Flora of North America" which will make it possible for all workers on this continent to become acquainted with the moss flora, and to utilize it in ecological work as it has so effectively been used for a long time by European botanists.

Cain: The use of the range of *constant* and *characteristic species* to determine the range of a union, or an association, is not entirely reliable. It is uncertain that two species growing together in the same union in Estonia are also associated in a community elsewhere, even though reported by the taxonomist from that region. In mapping the range of constant species, one must ask where their constancy was ascertained. Likewise the characteristic species, though characteristic species in Estonia, will not necessarily be characteristic species at a sufficiently great distance from Estonia. If the maps of the constant and characteristic species of the hemicryptophytic-cryptophytic union of the summergreen forest of Asia were prepared by some phytosociologist in Eastern Asia,

they would show a center there and a decrease in extent westward, the reverse of the speaker's maps.

The occurrence of the union can be mapped only in such places from which it is known with the same *characteristic* and *constant* species.

Lippmaa: That the method is applicable beginning with analyses carried out in a small country like Estonia is proved by the fact, that the area thus obtained coincides with the results which may be obtained from the literature dealing with the forest vegetation of Europe and northern Asia. Obviously, the Galeobdolon-Asperula-Asarum union does not exist in the Far East.

Cain: Another answer to my question would be the very great likelihood that the characteristic and constant species of the *Galeobdolon* union will be found together in most places, because they have very similar requirements.

Lippmaa: International collaboration in mapping species which are most important for the study of some communities would undoubtedly be of immense service.

Carpenter: An important item to be included on such maps is the local habitat occupied by a species.

Lippmaa: The literature upon which my map is based includes many sociological studies covering the area from Japan to England.

The Climax and Its Complexities*

Stanley A. Cain**

CONTENTS

I. Introduction ---- 147
II. What is a plant community? ---- 147
III. A brief conspectus of Clements' concepts and terminology of the climax ---- 150
IV. The complexity of the climax ---- 152
A. The structure of the climax ---- 152
1. Chorological complexity of the climax ---- 152
2. Chronological complexity of the climax ---- 153
3. Internal structural complexity of communities ---- 154
a. Synusial structure ---- 154
b. Quantitative relations within the community ---- 156
B. The causes of variability within the climax ---- 158
1. The physical causes ---- 158
2. The biotic causes ---- 159
V. Special considerations ---- 162
A. Twin associations ---- 162
B. Ecological series of associations ---- 167
C. The association-segregate ---- 169
D. Tertiary relicts and the climax problem ---- 170
E. The monoclimax, the polyclimax, and retrogression ---- 172
VI. Concluding statement ---- 175
VII. References ---- 176
Acknowledgements ---- 176
Discussion ---- 181

* Contribution from the Department of Botany, The University of Tennessee, New Series No. 30.

** The University of Tennessee and The Biological Laboratory.

I. Introduction

No biologist doubts the existence of individual socially integrated communities—the stands, the association-individuals, the biocoenoses—in their concrete expression at a certain place and at a certain time. The facts concerning the individual community are definite; but descriptions of communities are seldom complete owing to the complexity of community composition and structure, and to the narrow point of view of many investigators.

The association in the abstract, or community of any rank, is another problem. The confusion, misunderstanding, and diverging principles found among students of communities are nearly all related, not to the association-individual but to the association as an abstraction. Science requires the formation of concepts and scientific thought attempts clarification of these. Ideas of the association in the abstract are obtained by the selection of the common features of numerous association-individuals and synthesizing them into a "type." This does not mean that the association is a "pigeon-hole." In dynamic ecology the association is very large, but it is a concrete entity.

Because of the broad, more or less obvious features held in common, the numerous differences among stands frequently are neglected or minimized. The varying degree to which investigators recognize differences constitutes one of the main causes of divergence in community interpretation and classification. The other principal cause of divergence seems to be the varying emphasis placed on aspects of structure and processes in vegetation. Floristic, physiognomic, edaphic, and successional ecology all have produced systems of classification. This paper aims to describe the complexity of vegetation and thereby to suggest the necessity for comprehensive investigations; and to show, in part at least, wherein various interpretations coincide or diverge from one another.

Rübel says, "The fundamental need of the human mind is for order, for grouping, so to be able to apprehend the infinity of things existing side by side. . . . We need a system of the plant communities of the world. . . . A classification may not be on a single factor, nor on a few factors. . . . All is relative." Schmid (1936) recently emphasized the highly complicated structure of the biocoenosis which can only be understood by an organized method combining the different approaches: the edaphic-physiognomic, the floristic-statistic, the biocoenologic, and the historic.

II. What is a Plant Community?

Community is a term of convenience which usually is employed to designate sociological units to every degree from the simplest one-layered aggregation to the most complex phytocoenosis. There are, however, certain aggregations of organisms which do not exhibit the characteristics generally attributed to a true community.

Alechin (196) says, "A plant community is a complex of plants with mutual adaptations. . . . It is obvious that the community is not made up of plants of one and the same life-form. . . . It is not correct that a community

is a group of plants showing the same adaptations. . . . When a pure community occurs, it may be because no ecological equivalent species is in the same region. . . . The fundamental characteristics of a plant community are: layering in space, layering in time [aspection], variability, stability." Paczoski (1917, quoted by Alechin, 1926) says, "Under community must be placed only such a plant complex as consists of elements of unlike value lawfully bound together, which build stable combinations (in variable equilibrium) and which can come to exist only in the course of a long time." According to Alechin (1926), Boris Keller states that with respect to the ecological and social qualities of communities, they must be divided into more or less marked plant groups. He calls them "Genossenschaften" (brotherhoods?) and claims that they have a certain independence and a uniform inner social structure. His "Genossenschaften" are in part phases or aspects, and in part layers; only the concept is ecological whereas the "Schicht" (society) can embrace two or more alternating "Genossenschaften." Alechin considers Keller's (1907) subdivisions of the phytocoenosis identical with the synusiae of Gams (1918). It would seem likely that they coincide with the unions of Lippmaa (1938). See also DuRietz (1936).

Lüdi (1928) believes that constance and fidelity are the most important community characteristics. (Constance is a purely structural unit, whereas fidelity, especially on the basis of a group of species, has diagnostic-indicative value.) At the same time a great importance must be attached to the genetic rôle of the species. The "aufbauenden" species are usually the dominants, but dominance is not a primary criterion for the demarcation of a community. Rübel (1936), also speaking of the association as the fundamental sociological unit, states that the species known as constants and characteristics are the main fetures of a community; they form the normal characteristic combination of species. Wangerin (1925) on the other hand claims that the basis of the community lies in the floristic assemblage but that its ecology is also important and it is correlated, in most cases, with the floristic assemblage. He considers the serviceability of purely statistical methods limited and sometimes misleading, and accordingly he leans toward the definition of the association given by Flahault and Schröter in 1910.

Tansley (1935) apparently postulates sociological integration as a characteristic of a community, for in criticizing the terms "organism" and "complex organism" as applied to a community (association), and in defending his term "quasi-organism" he says,

> It is precisely this mass action, together with the actions due to the close and often delicate interlocking of the functions of the constituent organisms, which gives coherence to the aggregation, forces us to call it a unit, justifies us in considering it as an organic entity, and makes it reasonable to speak of the development of that entity.

In describing the fundamental unity of the phytocoenosis, as opposed to the synusia, Gleason (1936) points out certain characteristics of communities. He finds that since its first recognition the community has always been considered a geographic unit. "It occupies space and it has boundaries. Moreover, it exhibits uniformity of structure within the area. . . . Without uniformity both extent and boundary lose all significance. . . . There must be a

boundary in time as well as in space; there must be a beginning as well as an end." Gleason states that the cause of uniformity is two-fold. "The first [cause] is the existence over a considerable area of an environment which is itself uniform. . . . The second is the existence throughout the area of a uniform type of physiological interference." By physiological interference Gleason refers to the "intersecting spheres of influence" of the plants of the community. ' 'In the plant community the essential nature, the fundamental cause, the real *ens* of its existence, is non-areal, while its manifestation is distinctly areal, characterized by uniformity, extent, and boundary."

Braun-Blanquet (1932) writes: "The community life of plants rests upon relations of dependency and commensalism; its universal and ever present expression is competition. Wherever the struggle for a place in which to germinate and to grow, or to obtain light or food, can be demonstrated, there is competition, there is relationship." Commensal organisms are those which enter into competition separately, whereas their common relation consists in the fact that they utilize simultaneously the various life conditions of a given habitat. Completely open stands of plants hardly can be considered true communities because there is no competition among them, no physiological interference. It must be remembered, however, that a community can be open above ground and yet be sociologically closed on account of root competition. Apparently Clements (1928) also excludes from true communities all aggregations which are strictly open: "Competition occurs whenever two or more plants make demands in excess of the supply. It is a universal characteristic of all plant communities, and is absent only in the initial stages of succession, when the pioneers are still isolated."

So far little has been said about animal members of communities, but it is probable that every community is a biocoenosis. In fact, the terms community and biocoenosis are actually synonymous, but both are so general that they have lost nearly all force. Communities may range all the way from the *biome* (of formational rank) to those of the smallest *biotope* (the life area of smallest space). As an example of investigations of the latter type of community (excluding microscopic communities), see Heinis (1937) who studied quantitatively the microbiocoenoses of *Sphagnum* polsters.

The following quotation from Alechin (1926) aptly concludes this section concerning the "requirements" for the recognition of a community.

> We place in a plant community a complex of plant species which has a definite structure and is composed of ecologically and phenologically different elements ("Schichtung" in space and time), which moreover—in spite of its mobility—forms a persevering system depicting botanically the physico-geogpraphic relations and the history of the region.

Plant groupings

I. Open
II. Closed
  1. Settlements ("Siedlungen," without social integration)
  2. Pure stands
    a. Temporary
    b. Enduring
  3. Communities

a. Dearranged equilibrium
b. Flowing equilibrium
c. Stable equilibrium
   a) Unsaturated (without the full complement of societies)
   b) Saturated.

Obviously sharp delimitations of the above cannot be drawn.

The nature of the plant community has always interested plant sociologists. Detailed discussions of this and related problems may be found in the following papers: Alechin (1925, 1926), Braun-Blanquet (1921, 1932), Cajander (1922), Carpenter (1936), Clements (1928), Däniker (1928, 1928a, 1936), Gams (1918), Gleason (1936), Katz (1930), Kylin (1926), Lüdi (1928), Phillips (1931, 1934), Scharfetter (1924), Shelford (1932), Sukatschew (1929), Wangerin (1922, 1925).

III. A Brief Conspectus of Clements' Concepts and Terminology of the Climax

The following statements derived almost entirely from a recent essay by Clements (1936) form the basis for subsequent discussions. Irrespective of how widely his concepts and terminology are accepted, he has evolved a philosophy, a group of principles, and a terminology which meet *nearly* every exigency.

The *climax* constitutes the major unit of vegetation and it is regarded as synonymous with *formation* and *biome;* it is considered a more or less permanent and final stage of a *complex organism* under the paramount control of climate. The visible unity of the climax is due to the life-form of the *dominants,* which is a concrete expression of the climate. Inasmuch as the climax constitutes the major unit of vegetation (or of the biosphere), it is often continental in extent. This being the case, the climax can not be expected to exhibit uniformity in biotic composition and sociological structure, on account of the gradual but marked shift in rainfall and temperature from one boundary of the climax to the other. What unity the climax has is dependent on the life-form of the dominants and on certain characteristic *genera* and families of plants and animals. Considerable differences in rank or territory occur among the dominants of each formation. *Perdominants* are those which, because of their wide range (not necessarily as dominants), link the associations of a climax. Within an association, the abundant and controlling species of a characteristic life-form are termed *dominants* and *subdominants* are the controlling species of a different life-form which belong to the inferior synusiae.

Although *development* is a primary characteristic of vegetation, *stabilization* is the universal tendency of all vegetation under the ruling climate and climaxes are characterized by a high degree of stability if reckoned in thousands or even millions of years. It is a fundamental part of Clements' concept that, given time and freedom, a climax vegetation of the same general type will be produced and stabilized, irrespective of earlier site differences. *Change* is constantly at work, but in primeval vegetation it is within the fabric of the

climax, and not destructive of it. *Aspection, annuation,* and natural *coaction* leave no permanent impress on the climax, but *successional changes* are an intrinsic part of the stabilizing process.

The hierarchy of climax units recognized by Clements consists of the following categories:

Climax (formation, biome)
- Association } Consociation
  - Faciation }
  - Lociation }
- Society
  - Sociation
  - Lamiation
- Clan

The *association* of Clements represents the primary division of the climax and differs entirely from what may be called the international interpretation as approved by recent Botanical Congresses (Du Rietz, 1929, 1930, 1930b, 1936). As the unity of the formation rests upon the wide distribution of perdominants, so the association is marked by one or more dominants peculiar to it, and by differences in rank and grouping of dominants held in common.

The *faciation* is the concrete subdivision of the association, the entire area of the latter being made up of the various faciations corresponding to particular regional climates within the general climate of the formation. Faciations appear to be geographical varieties of the association, or subassociations, related to temperature and rainfall variations in different portions of the area of the association.

The *lociation* is a subdivision of the faciation characterized by more or less local differences in the abundance and grouping of two or more dominants of the faciation. Lociations may depend in some part upon edaphic variations, within the area of a faciation, such as variations in soil, slope, exposure, altitude. Lociations occur frequently as *alternes* with each other and with proclimaxes.

The *consociation* is constituted by a single dominant. Since the actual area of the association is divided into faciations, and the faciations into lociations, the consociation is apparently a phytocoenosis with only one dominant. Mono-dominant lociations, faciations, and associations, i.e., consociations of all ranks can easily be conceived. The term consociation is therefore not important since one might well speak of 1-dominant, 2-dominant, 3-dominant, and poly-dominant locations, faciations, and associations, rather than to single out the 1-dominant phytocoenoses as consociations.

The term *society* is employed as a general term for all communities of subdominants, that is, for all synusiae or life-form groups below the dominant synusia. Societies partake of both space and time differentiation.

The *sociation* is an aspect society related to the life history of the subdominants and the seasonal march of the environment factors.

The *lamiation* is a layer society based on life-form and environmental differences within the phytocoenosis. The term lamiation appears less suitable

than synusia because the latter includes all subdominant life-form groups, whether in horizontal layers or not (corticolous, epixylic, epilithic societies), as well as the dominant community. It is probably over-emphasis of the dominant layer which causes American ecologists to separate it so definitely from subdominant layers. The term *union* is now proposed for these "einschichtige Pflanzenvereine" (Du Rietz, 1936).

The *clan* is a small community of subordinate importance but commonly of distinctive character. It is marked by high density and efficiency in competition of the dominant plants resulting from vegetative reproduction by rhizomes, stolons, corms, bulbs, tubers, etc.

It is essentially a patch or a consociation.* Although clan is usually applied to members of the field layer, the dynamics of clan formation may occur also in bryophytic, frutescent, and arborescent societies. Consequently, the idea of consociation can be applied to all other life-form subdivisions of the phytocoenosis. Thus the consociation apparently is not a fundamental unit of the climax.

IV. The Complexity of the Climax

A. The Structure of the Climax

1. *Chorological complexity of the climax*

The earth's surface is covered by relatively few world formations (Rübel, 1930, 1936) such as rain forest, summergreen forest, grassland, etc., each covering thousands of square miles and possessing a fundamental life-form unity, — the climaxes (formations, biomes) of Clements. Speaking of North America, Clements (1936) says:

> The visible unity of the climax is due primarily to the life-form of the dominants, which is the concrete expression of the climate. In prairie and steppe this is the grass form, with which must be reckoned the sedges, especially in the tundra. The shrub characterizes the three scrub climaxes of North America, namely, desert, sagebrush, and chaparral, while the tree appears in three subforms, coniferous, deciduous, and broad-leaved evergreen.

Weaver and Clements (1938) recognize only 12 extra-tropical climaxes for North America.

Within a climax formation, however, there are many different communities variously treated and designated by different authors. For example, Rübel (1932) lists for Switzerland 169 communities (133 associations and 36 subassociations) grouped into 54 orders and 31 classes, whereas Conard (1935) enumerates about 70 associations for Central Long Island. On the other hand Weaver and Clements recognize only 29 associations for all of extra-tropical North America. Undoubtedly numerous different stands of vegetation exist within a climax; consequently the difference of interpretation

* In correspondence Clements states, "It seems best to restrict consociation to single extensive dominants, such as *Picea engelmanni* in the Front Range of Colorado, *Pinus pondorosa* in the Southwest, *Picea alba* in the western part of the boreal forest, etc. Naturally, in associations of several or many dominants, they are lacking or relatively rare."

must be largely due to the differences between static and dynamic treatments.

The beech forects of Europe probably have been studied more intensely by a group of plant sociologists than any other single complex type. Careful reading of "Die Buchenwälder Europas" (Rübel, 1932) reveals two important points: 1) the fundamental variability in composition and structure of the beech forests of Europe and 2) that despite an organized plan of investiagtion, differences of method hinder greatly the comparison of results and descriptions.

Within the climax, Clements recognizes a small number of associations which are divided chorologically into faciations and lociations, occupying progressively smaller areas. In original vegetation the associations showed some interdigitation according to the influence of topography on climate; the faciations represented geographical subassociations and zones, and the lociations undoubtedly appeared as belts and alternes within the faciations. The patchwork nature of vegetation is further complicated by the fact that not all vegetation is in the climax state since in all physiographically young regions and in disturbed areas occur numerous seral stages, slowly on their way to stabilization.

Moreover, relatively stable communities neither actively developing nor true climaxes, represent the proclimaxes of Clements, namely, subclimaxes, and disclimaxes. See also Tüxen (1937) and Ciferri (1936). Seral communities, climatic climaxes (lociations and faciations), and the various deflected (Godwin, 1929) and edaphic climaxes of Nichols, Tansley, et al., all have been regarded as associations. Whatever their rank, they compose a tremendously complicated chorological pattern of vegetation.

An association-individual, regardless of rank, is concrete, but the association itself is a concept to the extent that different stands of an association lack identity. The farther apart the stands the more different they become in composition and structure so that the extremes hardly represent the same "association," except as broadly conceived by Clements.

2. *Chronological Complexity of the Climax*

Vegetation is complicated not only in space but also in time. Cooper (1926) emphasizes the fundamental nature of change in vegetation and Clements (1936) says, "No one realizes more clearly than the devotee of succession that change is constantly and universally at work, but in the absence of civilized men this is within the fabric of the climax, and not destructive to it. . . . It can still be confidently affirmed that stabilization is the universal tendency of all vegetation under the ruling climate." See also, Phillips (1934).

Vegetational development has long been recognized as consisting of series of communities (associes) which can be grouped into xeroseres and hydroseres, according to the relative dryness or moistness of the primary condition, leading toward a climax under conditions of relative mesophytism for the given climate. Polunin (1936) wanted a term to describe certain conditions found in the Arctic; "In considering dynamic ecology of many regions, at least in the Arctic, it seems necessary to distinguish a mesosere, or succession starting

with the colonization of suitable bare areas, neither by hydrophytes nor by extreme xerophytes but, instead, by some of the more mesophytic plants existing in the region." Moreover, a condition of relative mesophytism must not be always the end of the successional tendency. Bourne (1934) says, "Confusion has followed from the assumption that the climax must be relatively mesophytic, no allowance being made for degradation of the habitat. . . . Clements has failed to realize that a mature soil in many climates is relatively degraded. . . . He has clearly had no experience of either podsol or laterite soils." At any rate, autogenic and allogenic successions (Tansley, 1935) add tremendously to the complexity of the vegetational pattern.

To these successions must be added the secular changes of the clisere which lead, especially in ecotonal regions, to an abundance of relict preclimax or postclimax communities. Clements (1916) defines a clisere as a series of climax formations or zones which follow each other in a particular climatic region subsequent to a distinct change of climate.

Still another group of successions are those of the *serule,* including a great variety of short, relatively swift successions starting on such bare substrata as bark, rotting wood, rocks, cadavers, etc. Oliver (1930) describes such successions among corticolous New Zealand epiphytes, whereas Cain and Penfound (1938) and Cain and Sharp (1938) recently called attention to such successions among bryophytes.

Other chronological complications in vegetation, such as those introduced by aspection and annuation, are discussed in connection with synusial structure.

Although American and British workers generally are concerned with successional phenomena certain papers in the field less familiar to Americans can be recommended: Braun-Blanquet and Jenny (1926), Ciferri (1936), Furrer (1922), Lüdi (1920, 1921, 1930).

3. *Internal Structural Complexity of Communities*

a. *The synusial structure of vegetation.* — Alechin (1926) emphasizes that the division of a phytocoenosis into layers is its first noticeable characteristic. A plant community is a complex of plants with mutual adaptations, and the layers indicate a form of this adaptation. Salisbury (1931) says that "The restriction of the concept of physiognomy to that of the dominants of a community is really to characterize the whole by a part that commonly represents a single stratum. The physiognomy of the dominants is often, in fact, that of a partial habitat." The recognition of the importance of layers in the structure of vegetation goes back, at least, to Hult (1881) whereas a system of organization of plant and animal life on a basis of life-form groups (synusiae) was proposed by Gams (1918). Obviously much of the complexity of communities is due to the fact that each biocoenosis usually is composed of many synusiae. Consequently, many systems of community classification ranging all the way from extremes in which only the dominant layer in considered to systems based primarily on the field layer (Cajander and the Finnish School) have been proposed. Other examples are the unistratal system of Lippmaa and the complicated twin associations of the Russians.

Plant associations show stratification above ground as well as in the soil. Therefore some investigators have arranged the communities of a region on a basis of sociological progression (Braun-Blanquet, 1932; Conard, 1935) proceeding from the simplest one-layered to the most complex many-layered associations. Mats of algae, moss, and lichens on soil, rock, and bark usually are considered one-layered (without rooting), but even these communities are likely biocoenoses of two or more synusiae. Heinis (1937), for example, studying quantitatively the microbiocoenoses of alpine plant polsters, did not find within the *Sphnagum* polsters an accumulation of dead organic remains but a complicated web of life based on food chains containing holophytes, herbivores, and carnivores, dominated by bacteria, diatomes, protozoa, and nematodes. In fact, in the detritus of these polsters he found 56 species including Flagellatae, Diatomaceae, algae, Ciliata, Rhizopoda, Rotaria, and Nematoda.

Forest phytocoenoses present the most complicated situations. Alechin (1926) states that temperate oak forests may have as many as seven layers, three of woody plants, three of herbaceous plants, and one of mosses. If the communities of all biotopes are included, the number of synusiae in a phytocoenosis becomes considerably greater. According to Lippmaa (1935), the Ulmus-Acer-Tilia association consists of five layers with six vertically distributed corticolous communities of bryophytes and lichens. The number of synusial communities would be even greater in forests with special biotopes such as erratic boulders, rotting logs, etc. The synusial complexity of many tropical rain forests is scarcely greater than that of temperate deciduous forests of mesophytic situations.

Subterranean root-layers also may be numerous, as shown by the extensive work of Weaver. Woodhead (1916) describes four root-layers in the forests of Huddersfield.

According to Alechin (1926), layering seems to be the result of long continued competition and at the same time of processes of adaptation. Layering results in the production of maximum plant mass on a definite surface and in the possibility of coexistence of plants of radically different ecological types. Competition is considerably more severe within a synusia than among members of different synusiae; the latter, consequently, are much less likely to destroy one another, but are able to reach a dynamic equilibrium. Such social integration apparently requires much time and as a result saturation, that is, a maximum number of societies, usually is found only in climax vegetation.

The development of synusiae in vegetation is really a four-dimensional matter. Alternating stands occur with changes in temperature and moisture from north to south and from east to west, as the case may be, in each layer of vegetation. The third dimension, of course, is layering and the fourth is time, as aspection and annuation.

Aspection refers to seasonal phases and every type of vegetation shows such rhythms. Some such phases are well marked by flowering periods and others by a radical shift in life-form. This time-"Schichtung" allows the development of a large number of ecologically different plants on the same

area. Alechin (1926) recognizes as many as 11 phases in the steppe near Kursk.

Annuation results from seasonal differences — a dry year following a wet one, weather conditions correlated with sun-spot cycles, etc. These influences are especially evident in grassland and desert where certain "ingredients" may fail completely for a series of years. According to Paczoski (1917; quoted by Alechin, 1926) this makes for "antagonistic plant groups" which flourish under different optima, occurring in time at the same place. In the steppe, legumes and grasses constitute such antagonistic groups. Iljinsky (1921; quoted by Alechin, 1926) found in a moist year on the steppe that grasses formed 66 per cent and legumes 2.3 per cent of the dry weight; whereas in a dry year the grasses formed 50 per cent and the legumes 18 per cent. A description of vegetation without consideration of time variation is clearly an approximation.

Certain plants find their required habitats only in association with other plants. This is essentially true of the hemicryptophytic-cryptophytic union of north temperate deciduous forests (Lippmaa, 1938). Certain inferior synusiae occur in many places associated with quite different superior synusiae. Recognition of these facts led Lippmaa to his emphasis on the unistratal community now called a union. Keller (1927), for example, in describing the vegetation of the plains of Russia, says: "The most important type of virgin spruce forest is the *Piceetum hylocomiosum*, the soil of which is characterized by a thick unbroken moss covering consisting of the following species: *Hylocomium proliferum* (= *H. splendens*), *H. triquetrum* (= *Rhytidiadelphus triquetrus*), *Hypnum Schreberi*, *H. cristacastrensis*, *Dicranum undulatum*. These mosses grow very well together and form a remarkably independent community, which may exist in association with various conifer trees": *Picea excelsa*, *Pinus sibirica*, *Abies sibirica*, *Larix sibirica*, *Pinus silvestris*. Essentially the same soil layer is characteristic of other conifer forests such as the *Picea rubens-Abies Fraseri* forests of the Southern Appalachians (Cain and Sharp, 1938). Cain (1934) pointed out that the small tree synusia of *Cornus florida*, *Cercis canadensis*, *Ostrya virginiana*, and *Carpinus caroliniana* occurs with a wide variety of forest types and associated herbaceous communities. It must be remembered, however, that the dynamic bonds are essentially vertical (Gleason, 1936) and that the lateral relations among plants of a synusia are relatively weak.

In conclusion, the development of synusiae is typical of all vegetation. The synusiae increase the complexity of vegetation but at the same time give it order. They are the practical units for investigation, because of their relative structural and ecological homogeneity. No study of a plant community can be considered complete unless it takes into account the synusiae.

b. *Quantitative relations within the community.* — The richness of its flora is certainly a characteristic of the community. Lippmaa (1932) says that, given time for stabilization, a certain number of species (variable within limits) is characteristic for a certain community. He cites the following: *Festuca ovina* association, 40 species; *Meum-Anemone* meadow, 52 species; *Tricho-*

phorum meadow, 14 species, for minimal areas of 50, 8, and 2 sq. m., respectively. Cain (1935) found *Piceetum rubentis* to consist of 9 tree species and *Abietum Fraseri* of 5. A stand of virgin hardwood forest, dominated by *Liriodendron tulipifera-Quercus alba-Acer saccharum-Nyssa sylvatica* consists of 32 species of trees, 9 shrubs and 105 herbs (Cain, 1934). Several of Conard's (1935) seaside associations, such as *Spartinetum patentis,* are composed of only 4 to 6 species each. At the other extreme stand certain tropical rain forests, each with a very large flora. Richards (1936) reports in the climax montane rain forest, on a plot of less than 4 acres, a total of 130 species of trees. Brown found 290 species of trees on 2.5 acres in the Dipterocarpous forest of the Philippines. In every case, however, the species number must be taken only in a general way.

Mere lists of species cannot give more than a very poor idea of the complexity of a piece of vegetation. Every description of a plant community should consider the density and manner of distribution of the plants of each species. Density, frequently estimated under the name of abundance, should be distinguished clearly from dominance, the area or space covered by the plants. The homogeneity of the community depends on the regularity with which plants of each species reoccur. Usually it is expressed by the term frequence (local constance) and constance (occurrence in quadrats from several stands of the same type). Homogeneity tends to develop because of the random nature of the distribution of propagules and of biotopes within a community. On the other hand, heterogeneity tends to develop as a result of the sociability, or gregariousness, of plants, especially those with vegetative methods of reproduction, with the resultant mosaic nature of vegetation. A discussion of these concepts is found in Braun-Blanquet (1932), in a résumé by Cain (1932), and Alechin (1932) gives a good review of the methods of the Russian phytosociologists.

Often minimal area is regarded as a characteristic of the community. Cain (1938) has recently considered minimal area, that area necessary for the development of the characteristic combination of species. In some bryophytic communities, this area may be as small as 0.1 sq. m. or less. For associations dominated by trees, it may be as large as a few thousand sq. m. Stands smaller than the minimal area are likely to be fragments of the association, without the characteristic combination of species (constant-dominants and species of high fidelity).

Salisbury (1931) believes that "the concept of minimal area cannot be given a very precise meaning and, though perhaps affording a convenient method of indicating differences in special cases, it is doubtful if it affords any additional information to that furnished by other data." In many tropical forests with a very rich flora and in certain African scrub communities described by Adamson (1931), the species-area curve used to indicate minimal area will not flatten out on account of the lack of species dominance. In these communities there is usually physiognomic dominance (Cain, 1932) and sometimes generic or family dominance. Richards (1936) describes the dominance (60 per cent) by Dipterocarpaceae in the rain forest but with no one

species attaining anything approaching dominance. In such cases, minimal area does not exist as the least area on which a characteristic combination of species can develop, or else it is exceedingly large.

The numerous aspects of community structure offer different criteria for the recognition and delimitation of communities. The available systems range from those emphasizing physiognomy to those based on ecology or floristic assemblages. Either the dominants are regarded most important or the key species are those of high constance or of high frequence. Braun-Blanquet bases his associations largely on species of high fidelity occurring primarily within the association type. However, in certain regions, such as the Sylene of Norway (Nordhagen, 1927), characteristic species with marked exclusiveness are almost entirely absent and constant-dominants must be relied upon.

Constancy and fidelity are both locally, but not generally valid. The composition and quantitative relations within an association change with the faciations. No association, except in the narrowest sense, has the same constant species throughout its entire range. Likewise, fidelity of a species to a community must be a rather local phenomenon since the same species will live under different conditions in different parts of its range and hence be associated with different communities.

B. The Causes of Variability within the Climax

1. *The Physical Causes of Variability Within the Climax*

Vegetation is under the master control of climate, particularly the climax, despite several other factors of temporary or local importance. Numerous excellent studies reveal the correlations between climate and vegetation (for example, Grisebach, 1872; Meriam, 1898; Livingston and Shreve, 1921; Szymkiewicz, 1923-7; Lundegårdh, 1931). Sharp boundaries are, of course, seldom found in nature and vegetation itself remains the best "integration" of climatic factors. That is, correlations of vegetation with temperature, light, precipitation, etc., as measured by meteorological methods are always difficult. All factors acting through the atmosphere, such as precipitation, light, temperature, humidity, wind, vary with reference to: amount, duration, extremes, means, periodicity, quality. Despite the many meanings of "climate" the fact remains that merging phenomena of extreme variability are involved.* Two regions never have exactly the same climate. Furthermore, within such a vegetation type as the American prairie, rainfall ranges from nearly 40 in. at the eastern edge to approximately 10 in. at the western border, or even to 6 in. in the desert plains, according to Clements (1936). Moreover, the growing period for the grasslands ranges from 9 months at the south to less than 3 months in the north, with mean annual temperatures of 70° and 33° F., respectively. The spruce-fir foramtion in the Great Smoky mountains has between 80 and 90 in. of rainfall on Clingman's Dome while in central Canadian regions it may be as low as 15 in. or less. It seems para-

* The climax, according to Clements, rests upon the response of the plant community and not upon that of man with his physical instruments.

doxical that climate is at once the great leveling or homogenizing influence and a primary cause of variability in vegetation.*

Topography contributes largely to the complexity of the vegetational pattern in any region affecting primarily the local climate, as well as the characters of the soil and the relations between climatic and edaphic factors: insolation, air temperature and soil temperature; precipitation and soil moisture, etc.

Physiographic activity causes change in vegetation through erosion and deposition (Cowles, 1899, 1901) and consequently increases greatly the complexity of the vegetational mosaic.

Soil, through its physical structure and chemical composition, determines to a greater or lesser extent the life it bears. Vegetation reacts on the soil (as it does on the microclimate) changing it through the addition of humus, increasing aeration, and in many other ways (Pallmann and Haffter, 1933; Braun-Blanquet and Jenny, 1926). Soil age is important, because under the joint action of climate and vegetation it takes on structure, and with time it reaches a mature or climax condition. In general such soil development results in "improvement" of the soil. In podsolization and laterite formation, however, the later stages of soil development are certainly processes of degradation, leading to a less mesophytic vegetation than that of the regional climatic climax. Soils vary to such an extent that no two square meters are exactly identical, yet it is possible to type soils and to establish numerous general correlations with both climate and vegetation (Glinka, 1927; Jenny, 1929; Thornthwaite, 1931). According to the mono-climax theory, the climate is supposed, given sufficient time, to harmonize all original differences among soils producing a uniform mature soil and climax vegetation. Recently several severe criticisms of this hypothesis were voiced by students of the vegetation and soils of Africa (Bourne, 1934; Michemore, 1934; Milne, 1936, 1937).

Still another cause of variability in vegetation is that of action and reaction. For example, under certain climates, evergreen vegetation contributes to an increased soil acidity and podsolization; and, with the resultant degradation of the soil (leached A-horizon with hardpan formation in the B-horizon), a new vegetation type makes its appearance. Another example is the formation of bog from forest by the reaction of *Sphagnum*.

2. *Biotic Causes of Variability Within the Climax*

The characteristic number of species in a community has been treated previously (see p. 156).

The idea of substitute species ("Vikaristen") and communities was introduced by Vierhapper (1919), referring to the fact that in different regions entirely analogous associations occur but with a different floristic composition. These substitute species and substitute associations, one would conclude, have

* Clements says, "the paradox is only apparent. For example, climate maintains grassland and terminates seres in it, but its subclimates, i.e. the cumulative effect of gradations, call out and are marked by the associations."

ecological equivalence. Du Rietz (1924) compares the vegetation of the Alps with similar Scandinavian communities. He compares some associations in which it would be impossible to distinguish statistical results from the two regions, whereas in the *Salix herbacea-Anthelia*-association more than half the species are identical and in the *Dryas*-heath the floristic composition is so different that one might well speak of two different associations. As an illustration of true substitutes he mentions *Empetrum nigrum*-heath of the northern hemisphere and *Empetrum rubrum*-heath in sub-Antarctic South America. The various species of *Picea* and *Abies* of the circumboreal spruce-fir formation would be considered true substitutes. Du Rietz says that according to Th. Fries the best example is found in Africa where on the different mountains entirely analogous associations occur whose species are all true substitutes.

By ecological ampliture is meant the inherent physiological nature of a plant which enables it to grow and reproduce within a certain range of environmental factors. Species differ physiologically just as they do morphologically. Although we know that in a general way structure and function are harmonious, it is certain, for example, that all xeromorphs are not xerophytes. Most biologists believe that, within certain limits, both structural and functional, new variations appear at random and that their survival depends on the fortuity of their appearance at the right time in the right place. That being the case, regions with the greatest variety of habitats might be expected to support the greatest variety of species because there is just as much chance that a new physiological characteristic will be of such a nature as to permit survival under one condition as another, although the chance is not as great that one condition will occur as another.

Furthermore, with respect to the range of any one factor of the environment, it is just as likely that a species will be fitted for one extreme as for another, or for any intermediate conditions. One might expect to find as many species capable of successful life at the extremes of environmental conditions as near the mean. This, however, is apparently not the case. In seres there are usually fewer species in the pioneer communities than in later stages of development; extremely xerophytic or extremely hydrophytic conditions do not support as rich a flora as do mesophytic conditions. The explanation probably rests on the fact that submarginal life conditions are not as widely found as "favorable" conditions. Consequently, new species will have a better chance to survive if they are constitutional mesophytes. Whatever may be the case, the flora of the spruce-fir formation, adapted to conditions submarginal to the summergreen forest, is apparently less rich than that of the latter. Similarly, the flora of the southeastern United States apparently consists of a larger number of species and varieties than the flora of a comparable area of the northeastern United States.

Certain conclusions follow logically. The richer a flora is in species the wider is the variety of physiological types which it presents. At the same time, however, it is also probable that more species have approximately similar requirements and consequently compete for the same space. Under such conditions, dominance of a community by one or two is less likely to occur than in regions where life conditions are submarginal.

Consequently, one of the major causes of variability among the communities of a climax is the difference in ecological amplitude. If a circle is used to illustrate the ecological amplitude of a species, then the species of a region represent a series of variously overlapping circles. The likelihood of two species occurring together at any one station is a matter of whether their "circles" overlap, and the extent to which they overlap. The ecological amplitudes of two species are neither identical, nor are the two species morphologically alike. Communities with single dominants seem to indicate the absence of ecologically equivalent species in the region.

A species of high fidelity, that is, one confined essentially to a single association, is likely to possess a narrow ecological amplitude. This is generally true of all good indicator species. However, a species which occupies a small geographical area may be either very young without sufficient time for migration, or old without the capacity for extending its range despite the availability of apparently suitable habitats; yet ecological isolation remains as another possible explanation.

On the other hand, species of broad ecological amplitude show low fidelity in any association and are frequently of wide geographic range, physiologically heterogeneous, and composed of many ecospecies.

In certain species one factor may vary within narrow limits whereas others have broader limits of variation. Such species can occupy only a comparatively small area and can grow in few communities, exemplifying the "law of the limiting factor." Actually the ecological situation is not quite as simple as that; aside from being able to grow under certain conditions, a plant must be able to reproduce and to compete successfully with other plants of similar requirements.

The ecological amplitude of a species for a factor may not be as great as it seems because of the possibility of substitution of factors; e.g., *Gaylussacia baccata* and *Acer rubrum* in *Sphagnum* swamps in Michigan and in dry, acid, pine heaths in Tennessee. Furthermore, a species may live under different conditions in two regions, being, for example, a calciphile in one place and a calciphobe in another (Salisbury, 1924).

Usually all factors are somewhat limiting simultaneously. Physiological investigations show that any factor in optimal condition modifies the effectiveness of every other factor. If 10 units of factor A are necessary for maximum growth of a plant, one unit will sustain 50 per cent growth, two units 75 per cent, three units 87.5 per cent, and so on according to the "law of diminishing returns." This is true for factors B, C, and all other factors affecting the growth of a plant. However, if all factors are present in sufficient amount for 100 per cent growth except A and B, present to the extent of one unit, each tending to permit 50 per cent growth, the result is not 50 per cent growth, but it is only 25 per cent of the theoretical maximum growth. Factor A allows 50 per cent growth and factor B allows only 50 per cent of that, i.e., the two together allow only 25 per cent growth.

Time is not a biotic factor but it is important in the action of two

causes of variability within the climax, evolution and migration. There is some evidence that the number of species in a flora depends partly on the time during which the area has been available for occupancy by plants, i.e., for evolution and migration. Thus many recently evolved species have not had time to reach their areal-ecological limits, e.g., some slowly migrating species in areas recently bare, such as the glaciated region of North America, although 20,000 years or more have passed.

V. Special Considerations

A. Twin Associations

In the classification of phytocoenoses involving more than the upper or dominating synusia several difficulties are encountered such as the structure of vegetation.

Gams (1918), a leading exponent of the synusial treatment, recalls that Hult (1881) investigated the composite nature of "formations" (phytocoenoses) with unsurpassed keenness and found important facts long overlooked. Hult described and named the layers of a phytocoenosis after their life-forms. He also realized that although the stand of one layer might remain constant over a considerable area, the stands of other layers frequently changed in composition. Such communities with changing patches (stands), but with at least a uniform dominating form, Hult called "tvillingsformationerna" (Zwillingsformationen, or twin formations). The common (mutual or joining) synusiae he designated "föreningsbestånd" (Verbindungsbestand, or combining stand); the changing synusiae he called "alternatbestånd" (Alternatbestände, or alternating stands). Gams goes on to explain that Hult spoke of *Pineta polymorpha* in which, for example, the combining stand was of *Pinus silvestris* and the alternating stands were of *Vaccinium myrtillus* and *Hylocomium* on the one hand and *Calluna* and *Cladina* on the other. The combining stand may be of another layer, as in his *Pineta-betuleta vagantia*, in which a layer community of *Hypnaceae* remains constant and the superior layer is made up of alternating stands of *Pinus* and *Betula*. Usually the alternating stands are of the same life-form but there are exceptions. For example, when the combining stand is of *Sphagnum*, the alternating stands may be of grasses and sedges, of herbs, or of shrubs. Also, in certain cases an alternating stand can fail without another taking its place, e.g., *Fagetum nudum*. All in all Hult knew 16 such twin formations and the results of his investigations were placed together in several sets.

The Russian phytosociologists (Keller, Sukachev, Alechin, Katz) found Hult's principles useful, developed and expanded the method to the recognition of "homologous series" of twin associations (see Katz 1929). They derive association names from the Latin names of the one or two dominants of each layer beginning with the upper layer. The layers are indicated in the association name by a separating dash (—), the codominants of any one layer by a plus (+). An example would be a four-layered association with two dominants in the second layer, such as the *Picea excelsa-Tilia cordata*+*Sorbus*

aucuparia—Aspidium spinulosum—Ozalis Acetosella—Association. Katz considers such names advantageous for he says, "the association name thus contains a short diagnosis and also gives a certain conception of the morphological structure and cites as examples the following:

Pinus silvestris-Ledum palustre-Sphagnum angustifolium-Association
Pinus silvestris-Cassandra calyculata-Sphagnum angustifolium-Association
Pinus silvestris-Eriophorum vaginatum-Sphagnum angustifolium-Association

It sometimes happens that one association is distinguished from another closely related one by the addition of a *"supplementary"* layer, as in the following example:

Pinus silvestris-Picea excelsa-Hypnum Schreberi-Associatien
Pinus silvestris-Picea excelsa-Vaccinium myrtillus-Hypnum Schreberi-Association.

Moreover Katz points out that "twin associations which are arranged according to the degree of their floristic similarity form *'the series of twin associations.'"* Such a series can be compared with *ecological series* (considered elsewhere in this paper), but the latter are not necessarily formed of twin associations. A few to several adjacent associations of the twin series, which are mostly distributed within a definite region, form the *"core of the twin series"* (Kern der Zwillingsreihe) and the associations themselves are referred to as *core associations* of the series. In addition, Katz says, "when the twin associations form at the same time vertical and horizontal series, these series are called *homologous* series." (This term is used here for the first time in plant sociology.)

Homologous series of twin associations have considerable significance with respect to the structure and ecology of vegetation. Katz draws his illustration from studies of central Russian *Sphagnum* moors. One series of twin associations is formed with *Sphagnum recurvum,* another with *Sphagnum medium,* as follows:

Pinus silvestris-Ledum palustre-Sphagnum recurvum-Association
Pinus silvestris-Cassandra calyculata-Sphagnum recurvum-Association
Pinus silvestris-Eriophorum vaginatum-Sphagnum recurvum-Association.
Pinus silvestris-Ledum palustre-Sphagnum medium-Association
Pinus silvestris-Cassandra calyculata-Sphagnum medium-Association
Pinus silvestris-Eriophorum vaginatum-Sphagnum medium-Association

Each association with *Sphagnum recurvum* (= *S. angustifolium*) is distinguished from the twin association of its series, in which *Sphagnum medium* dominates, by the higher constance of plants characteristic of mineral forest soils (*Vaccinium myrtillus, V. vitis-idaea, Hylocomium Schreberi*), or by more or less dry and decomposed peat (*Ledum palustre, Vaccinium uliginosum*). In brief, twin associations of the homologous series vary floristically in the same manner and hand in hand with the ecology (habitat). Thus, the position of an association in an homologous series gives a conception of its floristic qualities and of its ecology. This is well illustrated by Katz in the following diagram:

	A	B	C
1	Calluna vulgaris-Sphagnum fuscum-Association	Eriophorum vaginatum-Sphagnum fuscum-Association	----------
2	Calluna vulgaris-Sphagnum rubellum-Association	Eriophorum vaginatum-Sphagnum rubellum-Association	----------
3	Calluna vulgaris-Sphagnum magellanicum-Association	Eriophorum vaginatum-Sphagnum magellanicum-Association	Scheuchzeria palustris-Sphagnum magelanicum-Association
4	Calluna vulgaris-Sphagnum balticum-Association	Eriophorum vaginatum-Sphagnum balticum-Association	Scheuchzeria palustris-Sphagnum balticum-Association
5	----------	Eriophorum vaginatum-Sphagnum Dusenii-Association	Scheuchzeria palustris-Sphagnum Dusenii-Association
6	----------	Eriophorum vaginatum Sphagnum cuspidatum-Association	Scheuchzeria palustris-Sphagnum cuspidatum-Association

The floristic relations, at least insofar as dominants are concerned, are revealed by the arrangement of the above associations of the homologous series. Furthermore, ecological relations are also shown because the hydrophily of the associations increases from top to the bottom and from left to right. The *Calluna vulgaris-Sphagnum fuscum*-Association is characteristic of the driest sites (for the series) and the *Scheuchzeria palustris-Sphagnum cuspidatum*-Association of the wettest sites. Moreover, this table illustrates that twin series can be made up on a basis of any layer: in the vertical columns *Sphagnum* species form the alternating stands whereas *Calluna, Eriophorum,* or *Scheuchzeria* remain constant, as the case may be. In the horizontal columns twin series are formed with a *Sphagnum* series dominant in the combining stand. The core associations are as follows: A1, A2, A3; B3, B4; C4, C5, C6. The core associations occur more frequently than do those at one end or the other of a series. Associations corresponding to A5 and A6, and to C1 and C2 are not known to occur.

The two principal arguments for the type of treatment of the association problem given by Russian phytosociologists may be summarized briefly: 1) An association name should be made up of the Latin names of the dominant species of each layer since this practice records both the structure (layers) and the floristics (dominants) of the association. 2) Arrangements of associations into twin series, and especially into homologous series, reveals floristic affinities and ecological relationships existing among the associations.

However, if followed consistently, such practices lead to impossibilities. American ecologists, in the main, simplified their association names and, in the case of forest associations, usually employed only the names of dominant species of the superior arborescent stratum, e.g., *Quercus-Carya* association (Weaver and Clements, 1938), sugar maple-beech-yellow birch forest type

(Hawley, et. al., 1932), *Piceetum rubentis* (Cain, 1935), *Aceretum rubri* (Conard, 1935; Cain and Penfound, 1938). Conard (1935) included certain subordinate layers in some of his association names, viz., *Quercetum kalmietosum* (*Quercus montana-Kalmia latifolia*-Association) and *Aceretum osmundaceum* (*Acer rubrum-Osmunda cinnamomea*-Association). No American author proposed names for associations based on all layers. If this were done, the above names would be: for the 3-layered association, *Quercus montana-Cornus florida-Kalmia latifolia*-Association (Cain, 1936) and for the 4-layered association, *Acer rubrum-Clethra alnifolia*+*Azalea viscosa—Unifolium canadense—Mnium hornum*-Association. It would be possible also to name a number of twin associations for the phytocoesoses dominated by *Acer rubrum*. It is worth noting that the above association name contains 11 words. Many phytocoenoses in warm temperate and tropical regions consist of more than four layers. Furthermore, consistent adoption of this principle would require consideration of other synusiae equally typical but not forming horizontal layers, e.g., corticolous bryophytic and lichen societies. Such "names" for associations would indeed give an idea of the floristics and structure of the association, but are scarcely usable in print, and certainly unpronounceable.

On the other hand a name can be too short and consequently ambiguous to a varying degree, e.g., *Curvuletum* for *Caricetum curvulae* and the *Quercus-Carya* association of Weaver and Clements. The latter is particularly objectionable since there are dozens of species of *Quercus* and *Carya* which although found in a single region, vary widely in their ecology and hence never occur together. On the other hand, several species may be codominant in a single stand (locution of a faciation of an association of Clements). Thus the name can have little significance except in the most general terms unless they are made definite by usage, as for example in family names such as Solanaceae.

The successful application in northern Europe of the above principles and nomenclatural system is possible primarily because of the relatively simple vegetation of those regions. The tremendous number of long names which would result from the application of these principles to the vegetation of the Great Smoky Mountains, for example, can easily be shown.

A good example is a forest phytocoenosis consisting of five layers (ignoring non-stratified synusiae) such as the *Piceetum rubentis* (Cain, 1935). The superior arborescent layer is assumed to remain constant (the combining stand) and four different societies in each of the four layers (that is, four alternating stands in each inferior layer) are assumed possible. The result of this assumptive condition of the vegetation is a large number of twin series with a total possibility of 256 combinations — 256 "associations," each with a five-parted name. That the above assumptions are not based on a purely imaginative situation can be attested by anyone familiar with the spruce-fir formation in the Southern Appalachian and the following alternating stands can be readily suggested:

Combining Stand of *Piceetum rubentis*, red spruce association (in the larger use of the term)

Inferior arborescent stratum (small tree layer)
1. *Abies Fraseri* society
2. *Betula allegheniensis* society
3. *Sorbus americana* society
4. *Prunus pennsylvanica* society
— Alternating Stands

Frutescent stratum (shrub layer)
1. *Rhododendron carolinianum* society
2. *Rhododendron catawbiense* society
3. *Hugeria erythrocarpa* society
4. *Menziesia pilosa* society
— Alternating Stands

Herbaceous stratum (field layer)
1. *Oxalis montana* society
2. *Dryopteris dilatata* society
3. *Aster acuminatus* society
4. *Clintonia borealis* society
— Alternating Stands

Cryptogamic stratum (soil layer of mosses and lichens)
1. *Hylocomium splendens* society
2. *Rhytidiadelphus triquetrus* society
3. *Polytrichum ohioense* society
4. *Cladonia squamosa* society
— Alternating Stands

All of these species are certainly dominant locally, but the author is not sufficiently familiar with their ecology to propose them as definite societies (or unions; see Lippmaa, 1938). However, assuming that these species are dominants of societies, the treatment of the resultant five-layered combinations as twin associations, forming twin series and homologous series would lead to 256 names, as illustrated below:

Picea-Sorbus-Menziesia-Oxalis-Hylocomium-Association
Picea-Sorbus-Menziesia-Oxalis-Rhytidiadelphus Associaton
Picea-Sorbus-Menziesia-Oxalis-Polytrichum-Association
Picea-Sorbus-Menziesia-Oxalis-Cladonia-Association

Picea-Abies-Rhododendron Catawbiense-Oxalis-Hylocomium-Association
Picea-Abies-Rhododendron Catawbiense-Dryopteris-Hylocomium-Association
Picea-Abies-Rhododendron Catawbiense-Aster-Hylocomium-Association
Picea-Abies-Rhododendron Catawbiense-Clintonia-Hylocomium-Association

Picea-Sorbus-Rhododendron Catawbiense-Oxalis-Hylocomium-Association
Picea-Sorbus-Rhododendron carolinianum-Oxalis-Hylocomium-Association
Picea-Sorbus-Hugeria erythrocarpa-Oxalis-Hylocomium-Association
Picea-Sorbus-Menziesia pilosa-Oxalis-Hylocomium-Associatien

It is superfluous to enumerate more of these five-parted names, which are actually longer since the specific as well as the generic name of each dominant should be used. If the assumption is extended to include four alternating superior arborescent stands in the alliance, *Piceion*, the same 16 layer societies remaining, the result is the appalling total of 1,024 twin associations (or consociations; see Du Rietz, 1930, 1936; Carpenter, 1938).

These assumptions, and the resultant nomenclatural burden, appear at first completely absurd. The fact remains, however, that synusial communities are fairly numerous and that the best procedure in the study of a complex phytocoensis is the analysis of individual societies or unions. See Lippmaa (1933, 1934, 1935, 1938), Pastak (1935), Sirgo (1935), Gleason (1936), Cain (1934, 1936), Cain and Penfound (1938). In intensive studies, whether sociological, ecological, or a combination of the two, synusial communities must be recognized. As different stands of the same association are studied, new com-

binations of societies are found. Thus the orderly arrangement of these more or less varying phytocoenoses becomes a necessity and the whole problem of community taxonomy is inevitable. These combinations may be of academic interest only, but they also may have economic importance in forestry, as indicators of site quality (microclimatic and microedaphic conditions).

In the author's opinion, it is unnecessary and in fact rarely useful, to set up these twin associations. It suffices to deal with the identical situation according to the simpler method of Lippmaa (citation above) naming only the *unions*, their various combinations becoming apparent from the details of the published reports. The above assumptions, then, require dealing only with 16 short union names instead of 256 long twin association names! or in the case of four alternating tall tree stands, 20 union names instead of 1,024 twin association names.

Although there are certain advantages to the methods of these Russian phytosociologists in naming twin associations, twin series and homologous series, the same methods are impracticable in regions with rich vegetation. Treatment on a basis of *unions* offers nearly the same possibilities without incurring the nomenclatural burden.

B. Ecological Series of Associations

The Russian phytosociologists have made considerable use of arrangements of associations in *ecological* series. Usually such a series is based on changes of the habitat with respect to a single primary factor. For example, Alechin (1926) says, "On our inundated meadows occurs a whole series of communities which are distinguished by physiognomy and ecology and which often form a complicated mosaic. Each community is distinct, but together they form a definite system, the basis of which is the changing moisture of the substratum. They form an ascending or descending ecological series." He gives an example from Tambow:

1. Association of *Festuca sulcata*
2. Association of *Agrostis canina* or *Bromus erecta*
3. Association of *Alopecurus pratensis*
4. Association of *Alopecurus pratensis* and *Poa palustris*
5. Association of *Poa palustris*
6. Association of *Beckmannia eruciformis*
7. Association of *Glyceria fluitans*
8. Association of *Glyceria aquatica*.

The upper associations are above the zone of overflow, the lower associations are in the marsh region of inundation. With a cyclic change of water level, the whole series is shifted to one side or the other. According to Alechin Ramensky (1918) considers such situations as "Pflanzengesellschaften in fliessendem Gleichgewicht" (or as "veränderlich-stabile").

Parker (in manuscript) describes an interesting situation at Long Pond, south of Wading River, Long Island, New York. Several more or less xerophytic pine barrens plants are inundated due to cyclic changes in water level of the kettlehole lake. Although the orthodox stages of hydrach succession are fairly clear, there is a certain amount of marching back and forth of the communities "in fliessendem Gleichgewicht."

The best illustration, known to the author, of the treatment of plant communities in ecological series is that of Sukachev (1928) dealing with the spruce communities of European Russia. Sukachev recognizes five fundamental types of habitat of the spruce to which correspond five principal types of forest differing in their phytosociological structure and in the size of trees. Conspicuous are alternating stands of the inferior layers resulting in the following spruce forest phytocoenoses:

I. *Piceeta hylocomiosa* (relief adequately developed; site well drained; soils more or less nutritive loams, clays or sandy loams, not moory)
  1. Piceetum oxalidosum
  2. Piceetum myrtillosum
  3. Piceetum atragenoso-oxalidosum
  4. Piceetum polystichosum
  5. Piceetum empetroso-vacciniosum

II. *Piceeta polytrichosa* (relief less developed; sites feebly drained; soils similar to I but already somewhat moory)
  6. Piceetum polytrichosum
  7. Piceetum empetroso-polytrichosum

III. *Piceeta sphagnosa* (relief undeveloped, surface flat; site not drained; soils moory)
  8. Piceetum sphagnosum
  9. Piceetum caricoso-sphagnosum

IV. *Piceeta herbosa* (in bottom of depressions with moory soils but with running water)
  10. Piceetum fontinale
  11. Piceetum sphagno-herbosum

V. *Piceeta fruticosa* (sites with nutritive well-drained soils, for the most part in the neighborhood of limestone)
  12. Piceetum tiliosum
  13. Piceetum quercoso tiliosum

According to Sukachev, many of these communities can be arranged in ecological series. One series is observed in connection with greater moisture and humus, and lower aeration of the soil, starting with *Piceetum oxalidosum* (1) and terminating with *Pinetum* and the ultimate replacement of forest by bog. Intermediate communities are *Piceetum myrtillosum* (2), *Piceetum polytrichosum* (6), and *Piceetum sphagnosum* (8). *Sphagnum* is the "builder" of this series, and although the development of phytosociological integration in *Piceetum oxalidosum* has proceeded during thousands of years, nevertheless *Piceetum myrtillosum* is the starting point of the deterioration of the spruce forest. "If the impulse," says Sukachev, "is usually given by external factors, its whole further course is connected with a change in environment produced by the plant communities themselves. Thus their own action on the environment is the chief cause of the succession of communities in the series."

Another important ecological series of spruce forest types brough about by the conversion of broad-leaf forest to typical *Piceetum oxalidosum*. The broad-leaf species drop out in the following order: ash, oak, maple, lime (*Tilia cordata*), in connection with the replacement of grey and black forest soils by podsol soils. The series, starting with typical oak forests, progresses as follows: *Piceetum quercoso-tiliosum* (13), *Piceetum tiliosum* (12), *Piceetum atragenoso-oxalidosum* (3), *Piceetum polystichosum* (4), to *Piceetum oxalidosum*

(1). Sukachev claims, in view of all available literature, that the oak and its associates are supplanted by spruce as a result of the impoverishment of the soil due to the influence of the forest communities themselves.

The value of distinguishing ecological series of communities lies in their usefulness to show 1) ecological relations, 2) genetical relations, 3) the new types of communities to be expected, their characteristics, and their classification, and 4) phytosociological relations.

In addition to the ecological series, connected with a change of the nature of the soil within the limits of a definite region, another type occurs, the climatic-geographic series. Sukachev recognizes a certain subjectiveness in these two types of series but believes that these fundamental ideas must serve as guides in further investigation of new spruce communities; moreover, without confusion, different grades of communities can be distinguished and brought into a definite system.

Apparently, these investigators construct ecological series of communities which are successional and also series of communities which are climax. The latter probably represent the lociations and faciations of Clements (Clements, 1936). The various "retrogressive" successions, a phenomenon inadmissible by Phillips (1934) who insists that all succession is developmental, would probably be explained by Clements as follows: 1) The ecological series from oak forest to *Piceetum oxalidosum* represents a *clisere*. A clisere is the spatial series of climaxes that are set in motion by a major climatic shift" (Clements, 1936, p. 266). (2) The ecological series resulting in the replacement of *Piceetum oxalidosum* by*Pinetum* and ultimately by *Sphagnum* bog would probably be considered by Clements as a *disclimax*. Clements (1936, p. 265) defines disclimax as a result "from modification or replacement of the true climax, either as a whole or in part, or from change in direction of succession." This might appear to be an admission of *retrogressive succession* by Clements, but it is clear from conversations and correspondence that he recognizes only *retrogression* due to destruction.

C. The Association-Segregate

Recently a very interesting interpretation of climax vegetation has been developed by Braun (1935a, 1935b), that is, the explanation of the deciduous forests south of the glacial boundary (Kentucky especially) on a basis of numrous *association-segregates* from the Tertiary *undifferentiated deciduous forest climax*. The term undifferentiated deciduous forest climax refers to the *mixed mesophytic forest* climax as studied by several Ohio ecologists (Braun, 1916; Transeau; Sampson, 1930; Gordon, 1932). The new term, association-segregate, proposed by Braun (1935b) refers to space-time segregates of the ancient mixed forest evolved by conditions of the environment (Braun, 1935a), and it includes consociation, faciation, and lociation, regardless of the number of dominants in a stand. "It is a dynamic term implying something as to origin and relationship." Apparently these segregate climaxes may arise by two methods: 1) by the retreat of certain species, those persisting constituting the segregate; or 2) by differential rates of and capacities for migration of

species of the undifferentiated complex into regions of uniform or of various environment.

The idea of the segregation of deciduous forests was expounded previously by Gleason (1923). This explanation of the origin and relationships of the heterogeneity of the climax formations is accepted in part by Clements (1936, p. 257):

> In the case of deciduous forest and grassland. . . the problem of differentiation resolves itself into tracing the origin and relationship of the several associations. It has been suggested that the mixed prairie by virtue of its position, extent and common dominants represents the original formation in Tertiary times, an assumption reinforced by its close resemblance to the steppe climax. . . . It is not improbable that the mixed hardwoods of the southern Appalachians bear a similar relation to the associations of the modern deciduous forest (Braun, 1935b).

Braun pointed out that

> The American deciduous forest formation has never been adequately treated as is demonstrated by the prevalence and persistence of the idea of three associations or the "threefold differentiation of the formation" and the recognition of only "three related associations, namely: (1) maple-beech, (2) oak-chestnut, and (3) oak-hickory." (Weaver and Clements, 1938.) In actual practice, moreover, one is confronted by the fact of equivalence as to climax status of consociation, faciation and lociaition; by the fact that all three are segregates of a more complex community.

Briefly, the concept is that in Tertiary times north temperate regions were characterized by an extensive and comparatively homogeneous (mixed) deciduous forest, the so called Arctotertiary forest. This vast and equable region began suffering change with the desiccation of the continental interior on account of the elevation of the Cordilleras. North-south differentiation resulted from the development of the Pleistocene glaciations. Today the most extensive and the richest relicts of the old Tertiary forest are to be found in the southern highlands, the undifferentiated deciduous forest climax. Locally, contiguous with the undifferentiated climax, occur the association-segregates. Farther removed from this center, certain of the association-segregates now occupying extensive marginal areas constitute the associations proper. At least part of the need for the term "association-segregate" is met by Clements' earlier terminology and he says, in correspondence, "it seemed already better taken care of by the climatic proclimaxes and by faciation and lociation."

D. Tertiary Relicts and the Climax Problem

As mentioned previously, Braun (1935b) attempted to explain the equivalent nature of the climax associations found in the southern highlands on a basis of space-time segregation from the relict Tertiary forests of mesophytic habitats — an interpretation favoring the ultimate recognition of a rather large series of climax associations. She admits that the association-segregates are the equivalent of lociations and faciations in undoubted climax stands, and of subclimaxes in other instances.

Prior to a discussion of the Tertiary nature of the mesophytic hardwood forests of the Great Smoky Mountains, a recent paper by Lippmaa (1938) dealing with the area and age of an important European woodland herb union,

the *Galeobdolon-Asperula-Asarum-union,* may be considered briefly. Lippmaa says, "All character-species and constant-species of the union are ancient forest plants which are often of an isolated systematic (taxonomic) position and whose relatives dwell all over Eastern Asia, North America, the Himalayas, and in part also in the Caucasus and Southern Europe (as well as northern temperate Europe). . . . The species of the union already existed in the Tertiary, or they were represented by species which today are very closely related." In another place Lippmaa points out that "it is certainly not accidental that the area of the *Galeobdolon-Asperula-Asarum* union and *its relatives* corresponds so well with the area of the temperate Tertiary forests." This union is throughout in coexistence with the deciduous mesophanerophytic union and requires the microclimatic and edaphic conditions found in temperate deciduous woodlands.

The virgin hardwood forests of the Great Smoky Mountains probably represent the greatest aggregation of Tertiary species now in existence in North America and certainly the best relicts of the Arctotertiary forests. It is impossible at this time to prove the Tertiary nature of the species typical of these forests, but certainly the genera are almost all Tertiary. See Berry (1930) and Knowlton (1927). The modern world distribution of the genera was taken from Dalla Torre and Harms (1900). High percentages of the woody genera of the forests are known from Tertiary fossils in Tennessee and the southeastern States (primarily the Lower Eocene Wilcox flora). By comparing the distribution of recent genera with the distributions of those known fossil and recent, it is possible to conclude that almost the entire flora dates from the early Tertiary.

All of the 12 genera, with species of trees which are dominant or codominant in one or more of the hardwood forest types, are probably Tertiary. Of the remaining 12 genera of trees, 75 per cent are probably Tertiary. Altogether 19 of the 24 genera are known from Tertiary fossils in Tennessee and a total of 87 per cent are probably Tertiary. Of the 11 shrub genera, 8 are known from fossiles and all are probably Tertiary. Likewise, all of the fern genera are of Tertiary times or earlier. Of the 74 genera of herbs in the hardwood mesophytic forests, 84 per cent are probably Tertiary. All of the genera which provide dominant species to the herbaceous communities are probably Tertiary and 44 of the 48 genera providing species of highest constancy fall likewise into this category. Altogether, 116 genera are known from the authors' sample plot studies of these cove hardwoods forests of which 96 per cent are probably early Tertiary.

It should be emphasized that these genera have enjoyed a continuous existence in the general region of the Great Smoky Mountains, where they are now found dominant, since their appearance in the Late Mesozoic or Early Cenozoic. Expressed differently, a botanist familiar with our forest flora would not be "lost," or even consider himself in a strange country, were it possible for him to walk through the original Arctotertiary forests of fifty million years ago. Although some genera and many species no longer exist, at least in this region, and many species are new, yet our hypothetical botanist

would be quite at home, judging from the similarity of many of the fossil species to living species. The story records continuity rather than change — stability rather than evolution.

The ancient forests possessed probably a structure and an ecology similar to those of the remnants now known in the southern highlands. It is commonly assumed that the Arctotertiary forest was homogeneous throughout its farflung distribution in Asia, Europe, Spitzbergen, Greenland, southeastern United States, western America, and Alaska. Although this is apparently true in a general way, because of the long time available for migration and the lack of barriers, our impression of the details is probably false. It is pretty unsafe to reason from structure to function, since physiological mutations may be as numerous as morphological mutation and certainly they are not always coordinated. In other words, it seems reasonable to assume that the species composing the Tertiary floras of various times and places showed considerable ecological diversification and various ecological amplitudes. At the same time, although the conditions of life were relatively equable over large areas, undoubtedly regional differences in climate, in microclimate, and in soil existed segregating the farflung Arctotertiary forest into local "associations." That is to say, although our present undifferentiated deciduous forest climax is probably representative of the mesophytic forest of that ancient time, association-segregates probably were present then too. This statement, however, does not refute completely the validity of Braun's interpretation of our modern climax complex.

This discussion, however, relates in the main to the interpretation of the modern climax. North and west of the Coastal Plain, east of the Mississippi Embayment, south of the Pleistocene glaciations, an extensive upland was continuously available for occupancy by land plants even prior to the appearance of Angiosperms. Here, under a temperate climate, was set a vast stage where the drama of evolution unfolded its plot uninterruptedly. Through millions of years now an essentially similar climax deciduous forest formation maintained its dominance being only slightly affected structurally by the desiccation of the continental interior, the inundations of the Mississippi Embayment, the refrigerations of the Pleistocene glaciations, or the tilting off of the shallow seas, although many shifts in areas must have occurred.

E. Monoclimax, Polyclimax, and Retrogression

A detailed presentation of the monoclimax hypothesis has been given by Phillips (1934), who adequately disposes of certain objections to that theory, but not of all.

It should be emphasized that many criticisms of the monoclimax hypothesis resulted from incomplete understanding of Clements' point of view. The question of the climax, Clements says, seems to be partly one of definition, but rather more a matter of analysis. Phillips says:

> It is essential for the investigator to take into account such features as the following: 1) a climax is very rarely, if indeed ever, wholly uniform floristically and structurally; 2) relicts are often present, such as persistent *seral* stages, *pre-climaxes* and *post-*

climaxes; 3) *climax associations* making up the *climax formation* show *faciations* and *facies, lociations and locies climatically* determined, and *serations* edaphically determined; 4) climatic cycles with reflections in the climaxes occur; 5) a climax is a "veritable mosaic"—to use Clement's expression—more especially since the development of agriculture, pastoral and forestry pursuits by man.

Since support of the polyclimax hypothesis (Du Rietz, Nichols, Tansley, Gams, Gleason, Nordhagen, Scharfetter, Tüxen, Domin, Conard) rests largely on the recognition of *edaphic climaxes,* it should be stressed that Clements too recognizes edaphic climaxes in the concept of *seration.* Phillips (1934) quotes a personal communication from Clements as follows: seration is "a kind of local expression of the clisere to be found on the flanks of great mountain ranges. The clisere represents a sequence of climaxes that moves as a unit in the face of climatic changes, as though strung on a string, and the *seration* represents a similar but *edaphic* sequence such as one would meet in crossing a valley from the high lands on either side." Petrie, Jarrett, and Patton (1929) and McLuckie and Petrie (1926) have described what they take to be reversible seres of climax vegetation due to physiographic conditions, providing good examples of seration.

Clements has met exponents of the polyclimax hypothesis in the following ways: 1) chorologically different stable communities are considered to be faciations and lociations of an association; 2) chronologically different stable communities are disposed of as subclimax, proclimax, preclimax, postclimax, held in stability by a continuing repressive factor; 3) stable communities not of the climatic climax but due to biotic factors are disclimax, in part; 4) topographically different stable communities, different because of continuing edaphic factors are called serations; 5) variations due to different soil types within a geological formation, or to different geological formations, are recognized (Phillips, 1934, p. 564), apparently under the name of lociation. The polyclimax view includes many different things, while Clements uses a different term for a different thing. In skillful hands this yields a more exact and scientific system.

Several investigators recently called attention to *climax* communities correlated with soil differences. Richards (1936) described a Mixed forest on heavy clay and loam which is typical rain forest and a Heath forest on sandy soils which lives under similar climatic conditions. He says, "If Clements' system of vegetation classification is followed strictly, Heath forest should probably be considered a preclimax type. Such a view, however, would seem to force the facts into an artificial scheme, for as no change of condition can be imagined which would convert heath forest soil into a mixed forest soil, no succession actual or potential is involved in the relation of the two types." Davis and Richards (1934) described five climax forest types in the Moraballi Creek tropical rain forest of British Guiana which form an ecological series from the Mora on wettest sites to the Wallaba on driest sites. These five forests are under the same climatic type but they are held apart by site differences. The authors say, "There is no reason for believing that the soils on which they are found are not mature and that they show any tendency to become similar to that of the mixed forest" which is the mesophytic climax of

the region. Du Rietz (1924) commenting on the stability of vegetation not of the climatic climax, states, "It is entirely not proven and it is very improbable that, for example, a snow patch community will develop in the direction of a *Curvuletum* (the climatic climax of the region) and that the rock lichen associations of necessity must be beginning stages of a succession toward higher associations." Keller (1927) claims that some differences among the climax oak forests on the plains of Russia are due to permanent soil differences, those on solonetz soils without a single dominant species.

Since Clements recognizes such differences in stable vegetation due to soil as variations within the climax, most of the differences between the adherents of the monoclimax hypothesis and the polyclimax hypothesis are differences of *terminology*. Clements certainly recognizes the fact that within the climax as he conceives it, many communities lower than the association are stable and differ in structure and composition.

Only one important problem remains, retrogression due to autogenic causes. Many allogenic causes of retrogressive changes rightly can be attributed to destruction and, therefore, initiate secondary successions. Disturbances of this sort are changes of water table due to physiographic activity (erosion and deposition), degradation due to rabbits, etc. However, apparently authentic instances of degradation of the soil are known which are *due to plant reactions* under the general control of climate and which lead to retrogression of the vegetation, e.g., these changes lead to a lower life-form, the reverse of development. These facts cannot be explained by insistence on the organismal nature of vegetation or the philosophic argument that development must of necessity be progressive in the community as well as in the individual. First the reported cases of retrogression due to reactions must be proven false before such statements as "Succession is the result of biotic reactions only" and "Succession is progressive only" can be made (Phillips, 1934, p. 565).

Tansley (1935) argues that cases of destruction have been used erroneously as examples of retrogressive succession and that normally they would initiate a subsere. "But if on the other hand there is what Phillips would call a 'continuative' cause at work which gradually leads to the degradation of vegetation to a lower type it seems to me that the phenomenon is properly called retrogressive succession." He lists as clear examples of allogenic retrogressive succession: 1) change of forest to grassland under continuous grazing; 2) change of forest to heath under leaching and raw humus formation; 3) change of mesophytic to more xerophytic vegetation due to increased drainage; 4) change from a higher to a lower (life-form) type of vegetation with water logging.

Watt (1938) just published another study on the ecology of Breckland in which he describes retrogression, the primary causes of which seem to lie in the community itself. In the *Festuco-Agrostidetum,*

> The main point of interest is that there is no continuous progression up the inclined plane of seral development from simple to more complex community with a corresponding increase in soil organic matter, but that each stage consists of a series of progressive and retrogressive phases. The succession in short is wave-like or cyclic. The cause of the cyclic change is clear in the moss-lichen succession where the lichen carpet disinte-

grates following the decay of the anchorage provided first by living, later by dead *Polytrichum piliferum* shoots. But it is not at present clear why the number of *Polytrichum* shoots should decrease on a stable soil nor why *Argostis* should pass through these cycles of change. . . . But lest a wrong impression is given it may be as well to state now that the phenomenon is independendent of climatic cycles inasmuch as retrogression and progression take place simultaneously.

According to Sukachev retrogression occurs, because of reaction, in the change from broad-leaved to spruce forest, and in the change from *Piceetum oxalidosum* to bog.

In the Great Smoky Mountains, principally in the spruce-fir belt, numerous treeless areas called heath occur, dominated by members of the Ericaceae, the most common species being *Kalmia latifolia, Rhododendron, maximum, R. catawbiense,* and *R. carolinianum.* Clements (1932) considers these broad-leaved, evergreen shrub communities entirely attributable to destruction. The author attributed these communities, many of which apparently occur in the absence of fire, in part to reactions of the evergreen vegetation under the general control of the spruce-fir climate and to the secondary control of edaphic factors; consequently, they represent a change beyond the climax spruce-fir due in part to reaction and may be retrogressive. (Cain, 1930, 1931, and later unpublished field work.) It remains for intensive field work to prove this case.

VI. Concluding Statement

The complexity of climax vegetation cannot be analyzed by investigations of communities from a restricted point of view.

Clements' climaxes and associations are physiognomic-floristic groups of undoubted verity. He and other students of geobotany have laid the broad foundations of vegetational study in America. It remains for ecologists, foresters, and plant sociologists to carry out the local, detailed, and coordinated studies which will allow an interpretation and utilization of the maze of variations within these broad climaxes.

Although undoubtedly real, Clements' associations are so large and heterogeneous as viewed by the local investigator that they can be described only in the most general terms. Clements' disposition of the variations within the climax (or climax region) through the concepts of faciation and lociation, through subclimax, proclimax and serclimax, through seration, and through preclimax and postclimax presents a scientifically and philosophically sound system. A description and classification of all the stable (climax) communities of a region might necessitate dealing with all the above concepts. A very large number of investigators have chosen not to follow Clements in this but to treat all such cover-types as "associations". The plant sociologists go even farther and include successional communities (associes) under the term. This may have some justification if the seral nature of the communities is not proven. The result, however, is to include many different things under the term, whereas Clements has a different term for a different thing.

Many investigators, for practical purposes, apply the term association to smaller and more homogeneous units of the order approved by the International Botanical Congresses. Even under this convenient, if less scientific, system, investigators should make clear, when possible, the exact status of each "association"; whether cliseral, seral, edaphic, or a geographic subdivision. It would seem that the best that can be hoped for in the near future is an amalgamation of the advantages of the dynamic and the static systems. Plant sociological methods lead toward a much needed emphasis on thorough analytical studies of the smaller more homogeneous stands of vegetation: dynamic ecology provides the key to unlock the interrelations existing among them.

The need for detailed study of associations throughout their entire range is emphasized. Gleason's individualistic association concept may be correct for analytical purposes whereas abstract associational concepts are necessary for synthetic, and frequently for practical, purposes. The association, as a *type* of vegetation, may be quite impossible to define accurately. Detailed studies over a wide area may reveal that the normal or typical association-individual does not, and cannot, exist. The *normal* is that imponderable haunting ingredient in the statistical pudding which, for plant associations, may be a snare and a delusion. There is a tremendous gap between the stand and the Clementsian association, two units which all ecologists are willing to recognize. Between these small and large units lie the complex problems of community taxonomy.

ACKNOWLEDGEMENTS

The writer wishes to take this opportunity to thank Dr. Theodor Just, Editor of The American Midland Naturalist, for many helpful suggestions. It is a pleasure to express appreciation to Dr. F. E. Clements for the clarification of many points relative to his concepts and methods. If any misrepresentation of Dr. Clements' viewpoint remains in this contribution the author deeply regrets it.

REFERENCES

No effort has been made to give a complete bibliography, nor to infer that the papers cited here are always the best or earliest examples of a given type of work or point of view.

ADAMSON, R. S. 1931—The plant communities of Table Mountain. II. Life-form dominance and succession. Jour. Ecol. **19**:304-320.

ALECHIN, W. W. 1925—Ist die Pflanzengesellschaft eine Abstraktion oder eine Realität? Englers Bot. Jahrb. **60**,(Beibl. 135):17-25.

———1926—Was ist eine Pflanzengesellschaft? Ihr Wesen und ihr Wert als Ausdruck des sozialen Lebens der Pflanzen. Fedde Repert. spec. novar. reg. veg. Beih. **37**:1-50. (Transl. from the Russian by Selma Ruoff.)

———1932—Die ältere russische Steppenforschung mit besonderer Berücksichtigung der quantitativen Methoden. Beitr. Biol. Pflanz. (Cohn's Beträge) **20**:25-58.

APPALACHIAN FOREST EXPERIMENT STATION. 1935—Forest improvement measures for the Southern Appalachians. U.S.D.A., Tech. Bull. **476**:1-45.

BERRY, E. W. 1930—Revision of the Lower Eocene Wilcox flora of the Southeastern States. U. S. Geol. Surv., Prof. Paper **156**.

BOURNE, R. 1934—Some ecological conceptions. Empire Forestry Journ. **13**:15-30. (See also, review by Barrington Moore, Jour. Forestry **32**:894-5. 1934.)

BRAUN, E. L. 1916—The physiographic ecology of the Cincinnati region. Ohio Biol. Surv. Bull. **7**.

———1935—The vegetation of Pine Mountain, Kentucky. Amer. Midl. Nat. **16**:517-565.

———1935b—The undifferentiated deciduous forest climax and the association-segregate. Ecology **16**:514-519.

BRAUN-BLANQUET, J. 1921—Prinzipien einer Systematik der Pflanzengesellschaften auf floristischer Grundlage. Jahrb. d. St. Gallischen naturw. Gesell. **57**:305-351.

———1932—Plant sociology: The study of plant communities. (Transl. by Fuller and Conard) McGraw-Hill, N. Y.

BRAUN-BLANQUET, J. AND H. JENNY. 1926—Vegetationsentwicklung und Bodenbildung in der alpinen Stufe der Zentralalpen. Neue Denkschr. Schweiz. Naturf. Ges. **63**:175-349.

CAIN, STANLEY A. 1930—An ecological study of the health balds of the Great Smoky Mountains. Butler Univ. Bot. Studies **1**:177-208.

———1931—Ecological studies of the vegetation of the Great Smoky Mountains. I. Soil reaction and plant distribution. Bot. Gaz. **91**:22-41.

———1932—Concerning certain phytosociological concepts. Ecol. Monogr. **2**:475-508.

———1934—Studies on virgin hardwood forest. II. A comparison of quadrat sizes in a quantitative phytosociological study of Nash's Woods, Posey County, Indiana. Amer. Midl. Nat. **15**:529-566.

———1935—Ecological studies of the vegetation of the Great Smoky Mountains. II. The quadrat method applied to sampling spruce and fir forest types. Amer. Midl. Nat. **16**:566-584.

———1936—The composition and structure of an oak woods, Cold Spring Harbor, Long Island, with special attention to sampling methods. Amer. Midl. Nat. **17**:725-740.

———1936b—Synusiae as a basis in plant sociological field work. Amer. Midl. Nat. **17**:665-672.

———1938—The species-area curve. Amer. Midl. Nat. **19**:573-581.

CAIN, STANLEY A. AND WM. T. PENFOUND. 1938—Aceretum rubri: the red maple swamp forest of Central Long Island. Amer. Midl. Nat. **19**:390-416.

CAIN, STANLEY A. AND A. J. SHARP. 1938—Bryophytic unions of certain forest types of the Great Smoky Mountains. Amer. Midl. Nat. **20**:249-301.

CAJANDER, A. K. 1922—Zur Begriffsbestimmung im Gebiet der Pflanzentopographie. Acta forest. fennica **20**.

CARPENTER, J. R. 1936—Concepts and criteria for the recognition of communities. Journ. Ecol. 24: 285-289.

———1938—An ecological glossary. Univ. Okla. Press. Norman.

CIFERRI, R. 1936—Studio geobotanico dell'Isola Hispaniola (Antille). Atti d'Inst. Bot. d'Univ. Pavia. Ser. 4, **8**:1-336.

CLEMENTS, F. E. 1928—Plant succession and indicators. H. W. Wilson, N. Y.

CLEMENTS, F. E. ET AL. 1932—Climate and climaxes. Carnegie Inst. Wash., Yearbook **31**:214-217.

———1934—The relict method in dynamic ecology. Journ. Ecol. **22**:39-68.

———1936—Nature and structure of the climax. Journ. Ecol. **24**:252-284.

CONARD, H. S. 1935—The plant associations of Central Long Island. Amer. Midl. Nat. **16**:433-516.

COOPER, W. S. 1926—The fundamentals of vegetational change. Ecology **7**:391-413.

COWLES, H. C. 1899—The ecological relations of the vegetation of the sand dunes of Lake Michigan. Bot. Gaz. **27**:95-116, 167-202, 281-308, 361-391.

———1901—The physiographic ecology of Chicago and vicinity; a study of the

origin, development, and classification of plant societies. Bot. Gaz. **31**:73-108, 145-182.

DÄNIKER, A. U. 1928—Ein ökologisches Prinzip zur Einteilung der Pflanzengesellschaften. Beiblatt z. Vierteljahrsschr. d. Nat. Gesell. Zürich. Festschrift Hans Schinz: 405-423.

———1928a—Die Grundlagen zur ökologischen Untersuchung der Pflanzengesellschaften. Vierteljahrsschr. d. Naturf. Ges. in Zürich **73**:

———1936—Die Struktur der Pflanzengesellschaft. Ber. Schweiz. Bot. Ges. **46**:576-593, Festband Rübel.

DAVIS, T. A. W. AND R. W. RICHARDS. 1934—The vegetation of Moraballi Creek, British Guiana: an ecological study of a limited area of tropical rain forest. II. Journ. Ecol. 22:160-133.

DAVY, J. BURTT. 1935—A sketch of the vegetation and flora of Tropical Africa. Empire Forestry Journ. **14**:191-201.

DEL VILLAR, E. H. 1929—Geobotánica. Barcelona.

DU RIETZ, G. E. 1924—Studien über die Vegetation der Alpen, mit derjenigen Skandinaviens verglichen. Veröffentlichungen d. geobotan. Inst. Rübel in Zürich **1**:31-138.

———1929—Fundamental units of vegetation. Proc. Intern. Congress Plant Sci., Ithaca 1926, **1**:623-7.

———1930—Classification and nomenclature of vegetation. Svensk Botan. Tidskrift **24**(4):489-503.

———1930b—Classification and nomenclature of vegetation. Rept. Proc. (Sect. Abstr.) Fifth Intern. Botan. Congress, Cambridge: 72-77.

———1936—Classification and nomenclature of vegetation units 1930-1935. Svensk Botan. Tidskrift **30**(3):580-589.

FURRER, E. 1922—Begriff und System der Pflanzensukzession. Vierteljahrsschr. Naturf. Ges. Zürich **67**:132-156.

GAMS, H. 1918—Prinzipienfragen der Vegetationsforschung. Vierteljahrsschr. d. Naturf. Ges. Zürich **63**:293-493.

GLEASON, H. A. 1923—The vegetational history of the middle west. Ann. Soc. Amer. Geogr. **12**:39-85.

———1936—Is the synusia an association? Ecology **17**:444-451.

GLINKA, K. 1927—The great soil groups of the world and their development. Edwards Bros., Ann Arbor.

GODWIN, H. 1929—The subclimax and deflected succession. Journ. Ecol. **17**:144-7.

GORDON, R. B. 1932—The primary forest types of the East-Central States. Abstr. Doctor's Disser. 8, Ohio State Univ.

GRADMANN, R. 1909—Über Begriffsbildung in der Lehre von den Pflanzenformationen. Englers Bot. Jahrb. **43**(Beibl. 99):91-103.

GRISEBACH, A. 1872—Die Vegetation der Erde naach ihrer klimatischen Anordnung. Leipzig.

HAWLEY, R. C. ET AL. 1932—Forest cover types of the Eastern United States: Report of committee on forest types. Journ. Forestry **30**:451-498.

HEINIS, FRITZ. 1937—Beiträge zur Mikrobiocoenose in alpinen Pflanzenpolstern. Bericht über d. Geobotan. Forschungsinst. Rübel in Zürich **1936**:61-76.

HULT, R. 1881—Försök till analytisk behandling af Växtformationerna. Meddel soc. pro fauna et flora fennica **8**.

JENNY, H. 1929—Climate and climatic soil types of Europe and United States. Soil Res. **1**:139-189.

KATZ, N. 1929—Die Zwillingsassoziationen und die homologen Reihen in der Phytosoziologie. Ber. deutsch. botan. Ges. **47**:154-164.

———1930—Die Hauptgesetzmässigkeit der Pflanzengesellschaften und der Begriff der Assoziationen. Bull. de la Soc. d. Natural. d. Moscou N. S. **39**(1-2): 147-176.

KELLER, B. A. 1927—Distribution of vegetation on the plains of European Russia. Journ. Ecol. **15**:189-233.

KNOWLTON, F. H. 1927—Plants of the Past. Princeton Univ. Press.

KYLIN, H. 1926—Über Begriffsbildung und Statistik in der Pflanzensoziologie. Bot. Notiser **1926**:81-180.

LIPPMAA, T. 1932—Pflanzensoziologische Betrachtungen. Fedde Repert. spec. nov. reg. veg. Beih. **66**:88-95.

———1933—Taimeühingute Uurimise Metoodika Ja Eesti Taimeühingute Klassifikatsiooni Pohi jooni. (Referat, Grundzüge der Pflanzensoziologischen Methodik nebst einer Klassifikation der Pflanzenassociationen Estlands). Acta Inst. Horti Botan. Univ. Tartu. **3**(4):1-169.

———1934—La méthode des associations unistrates et la système écologique des associations. Acta Inst. Horti Botan. Univ. Tartu. **4**(1-2):1-6.

———1935—Une analyse des forêts de l'ile estonienne d'Abruka (Abro) sur la bade des associations unistrates. Acta inst. Horti Botan. Univ. Tartu. **4**(1-2):1-97.

———1938—Areal und Altersbestimmung einer Union (Galeobdolon-Asperula-Asarum-Union) sowie das Problem der Charakterarten und der Konstanten. Acta Inst. Horti Botan. Univ. Tartu **6**(2):1-152.

LIVINGSTON, B. E. AND F. SHREVE. 1921—The distribution of vegetation in the United States as related to climatic conditions. Carnegie Inst. Wash. Publ. **284**.

LÜDI, W. 1920—Die Sukzession der Pflanzenvereine. Mitteil. d. Naturf. Ges. in Bern a. d. Jahr 1919.

———1921—Die Pflanzengesellschaften des Lauterbrunnentales und ihre Sukzession. Beitr. z. geobot. Landesaufnahme **9**. Zürich.

———1928—Der Assoziationsbegriff in der Pflanzensoziologie. Bibliotheca Botanica **96**:1-93.

———1930—Die Methoden der Sukzessionsforschung in der Pflanzensoziologie. Handb. Biol. Arbetismeth. Abderhalden. XI. **5**:528-728.

MCLUCKIE, J. AND A. H. K. PETRIE. 1926—An ecological study of the flora of Mount Wilson. Proc. Linn. Soc. N. S. W. **51**:94-113.

LUNDEGARDH, H. 1931—Environment and plant develompent ("Klima und Boden in ihrer Wirkung auf das Pflanzenleben." Transl. E. Ashby). London.

MERRIAM, C. H. 1898—Life zones and crop zones of the United States. U.S.D.A., Bull. **10**.

MICHELMORE, A. P. G. 1934—Vegetation succession and regional surveys with special reference to tropical Africa. Journ. Ecol. **22**:313-7.

MILNE, G. ET AL. 1936—A provisional soil map of East Africa with explanatory memoir. Amani, T. T., E. Afric. Agric. Res. Sta.

MILNE, G. 1937—Notes on soil conditions and two East African vegetation types. Joourn. Ecol. **25**:254-8.

MOSS, C. E. 1910—The fundamental units of vegetation. New Phytol. **9**:18-53.

NICHOLS, G. E. 1917—The interpretation and application of certain terms and concepts in the ecological classification of plant communities. Plant World **20**:305-319, 341-353.

———1923—A working basis for the ecological classification of plant communities. Ecology **4**:11-23, 154-180.

NORDHAGEN, R. 1927—Die Vegetation und Flora des Sylenegebietes. Oslo.

OLIVER, W. R. B. 1930—New Zealand epiphytes. Jour. Ecol. **28**:1-50.

PALLMANN, H. AND P. HAFFTER. 1933—Pflanzensoziologische und bodenkundliche Untersuchungen im Oberengadin mit besonderer Berücksichtigung der Zwerg-

strauchgesellschaften der Ordnung Rhodoreto-Vaccinietalia. Ber. Schweiz. Botan. Ges. **42**:357-466.

PARKER, DOROTHY. 1938—Plant succession at Long Pond, Long Island. In manuscript.

PASTAK, ELSA. 1935—Harilaiu Taimkate (English summary, The vegetation of the Peninsula of Hariland, Estonie). Acta Inst. Horti Botan. Univ. Tartu. **5**(1-2):1-44.

PETRIE, A. H. K., P. H. JARRETT, AND R. T. PATTON. 1929—The vegetation of the Black Spur regiono: A study in the ecology of some Australian mountain Eucalyptus forests. I. Jour. Ecol. **17**:221-48.

PHILLIPS, J. 1931—The biotic community. Journ. Ecol. **19**:1-24.

———1934—Succession, development, the climax, and the complex organism: An analysis of concepts. Journ. Ecol. **22**:554-571; **23**:210-246, 488-508.

POLUNIN, NICHOLAS. 1936—Plant succession in Norwegian Lapland. Journ. Ecol. **24**:372-391.

RICHARDS, P. W. 1936—Ecological observations on the rain forest of Mount Dulit, Sarawak. I. Journ. Ecol. **24**:1-37.

RÜBEL, E. 1930—Pflanzengesellschaften der Erde. Hans Huber. Bern/Berlin.

———1932—Versuch einer Übersicht über die Pflanzengesellschaften der Schweiz. Bericht über d. geobotan. Forschungsinst. Rübel in Zürich: 19-30.

———1932—Die Buchenwälder Europas. Veroffentl. Geobotan. Inst. Rübel in Zürich. **8**:1-502.

———1936—Plant communities of the world. Pp. 263-290 of "Essays in Geobotany in Honor of William Albert Setchell." Univ. Calif. Press.

SALISBURY, E. J. 1924—The change in habitat of certain plants. Veröffentlichungen d. geobotan. Inst. Rübel in Zürich. **1**:285-8.

———1931—The standardization of descriptions of plant communities. Journ. Ecol. **19**:177-189.

SAMPSON, H. C. 1930—The mixed mesophytic forest community of northeastern Ohio. Ohio Journ. Sci. **30**:358-367.

SCHARFETTER, R. 1924—Die Grenzen der Pflanzenvereins. Festschrift für Robert Sieger: 54-69. Wien.

SCHMID, E. 1922—Biozönologie und Soziologie. Natur. Wochensch. N. F. **21**:518-523.

———1936—Was ist eine Pflanzengesellschaft? Schweiz. Botan. Gesell. Berichte **46**:565-575. Festband Rübel.

SIRGO, V. 1935—Emajoe Alamjooksul Peipsiäärsel Medalikul Asuvaist Taimeühinguist. (English summary, Plant unions of the swamps at the mouth of the river Emajogi.) Acta Inst. Horti Botan. Univ. Tartu. **4**(3-4):1-64.

SUKACHEV, V. N. 1928—1928—Principles of classification of the spruce communities of European Russia. Journ. Ecol. **16**:1-18.

SUKATSCHEW, W. 1929—Über einige Grundbegriffe in der Phytosoziologie. Berricht. d. deutsch Botan. Gesell. **47**:296-312.

SZYMKIEWICZ, D. 1923-1927—Études climatologiques. I-XIII. Acta Soc. Bot. Pol. 1-4.

TANSLEY, A. G. 1935—The use and abuse of vegetational concepts and terms. Ecology **16**:284-307.

THORNTHWAITE, C. W. 1931—The climates of North America. Geogr. Rev. **21**:633-655.

TRANSEAU, E. N. 1927—Vegetation types and insect devastations. Ecology **8**:285-288.

TÜXEN, R. and H. DIEMONT. 1937—Klimaxgruppe und Klimaxschwarm, ein Beitrag zur Klimaxtheorie. Jahresber. Naturhist. Ges. Hannover **88/89**:73-87.

VIERHAPPER, F. 1919—Über echten und falschen Vikarismus. Oest. Bot. Zeitschr. **68**:1-22.

WANGERIN, W. 1922—Die Grundfragen der Pflanzensoziologie. Die Naturwissenschaften **10**:574-582.

———1925—Beiträge zur pflanzensoziologischen Begriffsbildung und Terminologie. I. Die Assoziation. Fedde Repert. spec. novar. reg. veg. Beihefte **36**:3-59.

WEAVER, J. E. AND F. E. CLEMENTS. 1938—Plant Ecology. McGraw-Hill, N. Y.

WOODHEAD, E. W. 1906—Ecology of woodland plants in the neighborhood of Huddersfield. Journ. Linn. Soc. **37**.

YAPP, R. H. 1922—The concept of habitat. Journ. Ecol. **10**:1-23.

———1925—The interrelations of plants in vegetation, and the concept of association. Veröff. Geobotan. Inst. Rübel in Zürich **3**:684-706. Festschrift Carl Schröter.

DISCUSSION

Gleason: The speaker's explanation of the Clementsian view of associations was very interesting to me since I have never before been able to understand what Clements meant by association. We are both familiar with the vegetation of the Middle West, as for example, flood plain associations with elms, sycamores, upland associations with beech and sugar maple, another with black oak, or all three. Do they all belong to the climax association?

Cain: Clements recognizes for the whole summergreen forest three associations: oak-chestnut, oak-hickory, beech-maple. Beech-maple occurs in the northern part of the old Northwest, and eastward, the oak-chestnut surrounds it on the east and the south, oak-hickory surrounds it on the west and part of the south. In the region in question, Clements would say that the floodplain forest is subclimax to the regional climax of the deciduous forest climax of the region; but a flood plain forest in the prairie ecotone would be postclimax.

Gleason: As I understand it, much of Indiana lies south of the beech-maple, and west of the oak-chestnut. The climax vegetation there would be oak-hickory, but there are many places without oak-hickory.

Cain: In parts of southern Indiana, Illinois, and Ohio, most of the upland is dominated by oak-hickory. You may get deep, rich, moist, soil forest types, such as beech-maple, next to oak-hickory. Also in the climax there are "oak openings" of grassland. These two types would be postclimax and preclimax to the climax oak-hickory.

Carpenter: In regard to the community in question, Clements would certainly not call the vegetation of an edaphic flood plain forest climax in any sense. It is a different kind of community, a successional community dependent on local edaphic factors. As examples of postclimax I would give the Illinois prairie and the mesic (not hydric) maple forest in the Devil's canyon in western Oklahoma. This is a deep canyon and the coenosis is typical maple forest even to the millipede and snail fauna.

Conard: In Long Island what is the oak forest, what is the pine forest, and what is the Hempstead plain?

Cain: According to Clements, all of Long Island belongs to the oak-chestnut association despite the fact that parasites have eliminated the chestnut. The pine barrens and the Hempstead grasslands do not belong to the theoretical climax of this region. The grasslands of the Hempstead plain are held in a grass condition because of soil conditions and fire; the climate is obviously deciduous forest climate. The grasslands are proclimax; the pine barrens subclimax.

Social Coordination and the Superorganism[1]

Alfred E. Emerson

"A collection of individual notes does not in itself form a melody; the melody comes only when we produce a particular arrangement of the individual notes. Harmony, therefore, is produced by the mental activity which recognizes the proportional relationships between the multiplicity of individual parts."—KEPLER. (See Hjort, 1938, p. 28).

Introduction

It has long been recognized that there are various levels of organization to be found among living things (Conger, 1925; Brown, 1926). Whitehead (1925, p. 278) has extended the organismic concept beyond biology. He says, "The whole of science revolves around this question of enduring organisms."

An organized biological unit relatively independent of other units is considered a biological individual. Originally the individual unit must have been considered almost self evident, but the analyses of intraspecific organic units have acquainted us with types of individual entities such as genes, viruses, non-nucleated cells, nucleated cells, cell colonies, multicellular organisms with simple tissues, metamorphic individuals, colonial metazoa, multicellular organisms with organs, metameric individuals, aggregations, sex pairs, families, societies, and finally interspecific groups of various ranks. These ascending hierarchies of integrated units with their special characteristics form the basis of the concept of emergent evolution (Pepper, 1926; Wheeler, 1928a; Morgan, 1933; Wright, 1935).

After considering these various levels of organization, our concept of the individual becomes rather abstract and we have to redefine our term as a living entity exhibiting a certain dynamic equilibrium and maintaining a relative stability in time and space. The functional attributes of protoplasms, cells, tissues, larvae, organs, zooids, segments, castes, species, and communities have been major interests among biologists. Likewise specialists concentrating upon the various coordinating mechanisms, such as metabolic gradients, organizers, hormones, the nervous system, and mechanical integration, together with their gene and enzyme foundations, have established distinctive sciences. Physiologists and ecologists have studied phases of dynamic equilibrium, embryologists have traced the mechanisms of ontogenetic patterns of development, and the geneticists and evolutionists have outlined the mechanisms of the phylogenetic patterns of development.

Since the times of Plato and Thomas Aquinas, many men have claimed

1 I am indebted to the following men for valuable suggestions and criticism: W. C. Allee, C. M. Child, G. P. DuShane, C. R. Moore, W. F. Ogburn, T. Park, and S. Wright.

that societies had attributes of organisms (Adam Smith in Hjort, 1938, p. 209; Comte, 1830-42; Darwin, 1859; Spencer, 1860; Wheeler, 1911, 1928a, 1928b, p. 304; Huxley, 1912, p. 142; Ferrière, 1915; Patten, 1920, p. 377; Lameere, 1922, 1931; Dendy, 1924; Child, 1924; Gerstung, 1926; Sumner and Keller, 1927; Alverdes, 1927, 1932, 1937; Allee, 1931; Gregory, 1934, p. 2; Newman, 1936; Manwaring, 1938; Hjort, 1938).

Others have opposed the concept (Letourneau, 1895, p. 35; Coker, 1910, p. 203; Carrel, 1930, p. 216; Rabaud, 1937).

Without attempting to minimize the importance of the study of the parts at any holistic level, my object in presenting this paper is to show the ontogenetic and phylogenetic correlations between the organism and the insect society, to reexamine the evidence for considering the animal society a superorganism, and to indicate some of the biological significance of the concept. I have not attempted to review the facts supporting or refuting the organismic concept of human society (See Coker, 1910; Bristol, 1915; Child, 1924: Cohen, 1931, p. 386).

My emphasis will be upon biological mechanisms and entities. Many writers emphasize the psychic correlations, particularly between human societies and human personality (See Coker, 1910). Although this division is probably the result of a dualistic philosophy and may therefore break down through the modern study of biological psychology, I feel I have too few demonstrated facts upon which to build any concept of a social psychic personality of an insect colony (See Cohen, 1931, p. 388). Wheeler (1933, p. 134) applies *Gestalt* to the insect colony, but he uses physiological facts to substantiate his concept.

Division of Labor

A self sustaining biological unit must acquire the energy for life from the environment, must protect this energy from being exploited by other organisms, must maintain ecological position, and must reproduce its kind. The fundamental adaptive modifications adjusted to these biological necessities are to be found somewhat separated in the organism, and constitute the basis for the universal biological phenomenon of division of labor (Snyder, 1924; Hjort, 1938, p. 151, 206).

The castes of social insects show a striking parallelism to cellular division of labor. The reproductive castes concentrate upon the function of maintaining the species and establishing new superorganismic units (Fisher, 1930, p. 181), thus paralleling the gametes. They also produce the sterile castes, thus paralleling tissue primordia. The workers are the nutritive caste. They might be analogized with the gastrovascular system of the organism. They collect the stored energy from the environment, comminute the particles, digest the materials, transport the substances to other castes and young, and through direct feeding supply the other units in the colony with requisite energy. The worker thus establishes the trophoporic field (Wheeler, 1928b). They also transport waste products to the exterior. The workers perform another function

through their shelter building activities. The nests establish buffer lines between the internal and external environment, thus helping to maintain favorable nest environments. In as much as shelters are usually non-living, the worker might be analogized with the shell-secreting cytoplasm of the protozoan or the shell-secreting tissue of the mollusc.

In the more primitive social Hymenoptera, the worker is also the caste which defends the colony from external attack. In the more highly integrated insect societies of ants and termites, the defensive ability is more highly specialized in the soldier caste.

The defensive function of the soldier ant, like that in the solitary hunting wasp, is often linked with predatory adjustments. At times it is possible to separate the functions of attack and defense however. The phragmotic specialization of the soldier of the ant, *Colobopsis*, which plugs the entrance to the nesting cavity (Wheeler, 1928b, p. 190), and the activities of the soldiers of the vegetarian fungus-growing ants *(Atta)*, are examples indicating purely defensive adaptation, while the soldiers of termites are obviously wholly defensive.

All the major castes may be further subdivided for special functions. Various types of ergatoid and neoteinic reproductives are known, especially among the ants and termites. Workers are often polymorphic and in certain cases may perform different acts. In the leaf-cutting ants *(Atta)*, the smallest workers remain in the nest and tend the fungus gardens while those of larger size leave the nest to gather pieces of leaves. In certain instances, striking heterogonic or proportional differentiations among the polymorphic workers may be detected (Huxley, 1927, p. 156), as in the army ants *(Eciton)*. This may be referred to as an anisomerous evolutionary tendency (Gregory, 1934, p. 2; 1936, p. 313). Among the honey-ants *(Myrmecocystus)*, some of the workers store the sweet liquid collected from aphids in greatly extended crops. Any worker may become a "replete" under special circumstances after the adult stage is reached. Division of labor in the worker bee at different ages has been demonstrated (Rösch, 1925, 1927; Morland, 1930).

Soldiers may also show polymorphic evolution and development. Among the ants they arose as a product of phylogenetic specialization of the worker caste. Among the termites, they were the original sterile caste (Emerson, 1926) and arose before complete sterility became established (Heath, 1928). The most striking case of dimorphism among termite soldiers is to be found in the genus *Rhinotermes* of the American tropics. The large soldier possesses mandibles of the more conventional biting type. The small soldier has degenerate functionless mandibles, but the labrum is greatly extended and connected by a groove with the opening of the frontal gland in the middle of the head (Snyder, 1926, p. 534). This gland is highly developed and extends backward into the abdomen (Holmgren, 1909). A fluid is emitted from this gland during periods of disturbance, flows down the groove, and comes to rest upon the hairs at the tip of the labrum where it disperses through evaporation. It may be interpreted as a form of specialized gas defense. Experiments show that the small soldier will die far more quickly if placed in a corked

bottle than an equal volume of large soldiers or workers. Also the odor from the small soldiers is characteristically stronger than that detected from the large soldiers or workers. This specialized minor soldier of *Rhinotermes* has nothing to do with the phylogeny of the nasute soldier (See Emerson, 1926; Wheeler, 1928b, p. 186).

The castes of the social insects may be analogized with the protoplasms of the cell, the sterile castes having certain attributes of the cytoplasm and the reproductive castes having attributes of the nucleus. An even better analogy, however, might be with the tissues of the multicellular organism, the sterile castes paralleling the somatic cells and the reproductive castes paralleling the germ cells (Wheeler, 1911). Differentiation and specialization of parts would seem to lead to the higher general efficiency of the whole (Weismann, 1893, p. 597; Fisher, 1930, p. 175; Hjort, 1938, p. 151).

Ontogenetic Coordination and Integration

Child (1924) has emphasized that dynamic physiological order and integration determine the origin of the individual organism rather than the specific morphological constitution of the parts. I personally think that morphology may be used as an indication of complex and subtle physiological activities and functions, "structure being itself a process or equilibrium of reactions" (Hjort, 1938, p. 131). A variety of techniques have been used to indicate the types of integrating mechanisms in the individual organism and it is of interest to discover whether parallels may also be found in the animal society which may justify the concept of the superorganism.

Chromosomal Foundations of Integration

The rôle played by hereditary factors in ontogeny is engaging the attention of the physiological geneticists at the present time (Lillie, R. S. 1938). Wright (1934, p. 142) has outlined his opinion concisely in the following paragraph:

> It seems to me that the view toward which we are tending is that the specificity in gene action is always a chemical specificity, probably the production of enzymes which guide metabolic processes along particular channels. A given array of genes thus determines the production of a particular kind of protoplasm with particular properties —such, for example, as that of responding to surface forces by the formation of a special sort of semipermeable membrane, and that of responding to trivial asymmetries in the play of external stimuli by polarization, with consequent orderly quantitative gradients in all physiologic processes. Different genes may now be called into play at different points in this simple pattern, either through the local formation of their specific substrates for action, or by activation of a mutational nature. In either case the pattern becomes more complex and qualitatively differentiated. Successive interactions of differentiated regions and the calling into play of additional genes may lead to any degree of complexity of pattern in the organism as a largely self-contained system. The array of genes, assembled in the course of evolution, must of course be one which determines a highly self-regulatory system of reactions.

Except for sexual differentiation, the superorganism, at least in the case of bees and termites, would seem to rest upon differentiation of prospective potencies among organisms with the same general gene complex. Fisher (1930, p. 181) has pointed out that "the different offspring of a single queen cannot be genetically identical, for the factors in which their mother is heterozygous must segregate. Such genetic variability, however, * * * seems not

to be utilized in producing polymorphism." Chromosomal (and possibly Mendelian) differentiation usually seems to influence the determination of sex in the ants, bees and wasps (Whiting, 1935; Snell, 1935), which typically have haploid males and diploid females. Snell (1932) shows how eugenic efficiency is promoted by the haploid male in the social Hymenoptera (also see Wheeler, 1933, p. 130). The gene and chromosome complex is not different in the specialized tissues or in the male and female organs of a normally hermaphroditic or monoecious organism.

Chromosomal and gene complexes have several times been postulated as governing the differentiatnon of the castes of social insects (Imms, 1919, 1931, p. 65, 101). Following the studies of Thompson (1917, 1919, 1922), I once held the view (Emerson, 1926) that the castes of termites were determined prior to hatching and thus probably were genetically different. However, the work of Hare (1934) showed that the nymphs at the time of hatching could not be distinguished on the basis of characters used by Thompson.

Recently Wheeler (1937) has expressed the view, based upon a highly interesting series of sex and caste intergrades, that caste differentiation in ants is determined by chromosomal differences. Whiting (1938) (see also Gregg, 1938; Schmieder, 1938), however, inclines toward the trophogenic theory and interprets Wheeler's intercastes as the result of the deviation of the caste determining influence during development.

We conclude that the coordinating effects of the chromosomes and genes would seem to act in the superorganism as they act in the multicellular organism and caste development would seem to be caused by similar mechanisms to those influencing somatic development.

It should be pointed out, however, that there is a genetic heterogeneity involving sex differentiation in some plants and in many higher animals including all the social species. Both genetically differentiated sexes are incorporated into the social organism, particularly among termites. We have no good parallel to this situation in the individual multicellular organism.

Activity Gradients and Symmetry

Child (1924) shows how the primary pattern of symmetry in organisms seem to correlate with metabolic activity gradients. Symmetries of social organisms seem to be demonstrated in certain instances (Child, 1924, p. 283; Lameere, 1931, p. xxviii; Emerson, 1938), particularly in the nest structures.

The arboreal nests of certain species of *Nasutitermes* are rounded structures composed of particles of woody carton. Although spherical in outline, a structural differentiation occurs from the periphery to the thick-walled central portion, where the royal cell is found (Emerson, 1938, p. 262). We may thus speak of the spherical symmetry of these nests and assign the causative mechanism to the quantitative activity gradient of the worker behavior. The same workers doubtless build both the interior and the exterior. The materials are wood or dirt and excrement or salivary secretions. Various proportions (Holdaway, 1933) and various amounts of these ingredients explain

the physical and chemical differentiation. The focus of activity is the queen around which the royal cell is constructed. The queen thus constitutes a center of physiological dominance, to use Child's term. Secondary dominance may be found among the individual workers. Chen (1937a, 1937b) has shown a gradient in the behavior activity as well as an interindividual response in nestbuilding worker ants. The comparatively more active ant in a group initiated the cooperative building work and became the temporary leader. Leaders showed indications of higher metabolism, but strength of cohesion of a group of leaders was less than that of a group of followers. Active and inactive ants tend to retain their respective activity characteristics (Combes, 1937).

One may object to the parallelism drawn because the social organism shows a differential behavior gradient while the typical organism shows a physiological gradient. It is so obvious that the psychic behavior of an organism is a response to physiological states, and that in turn the psychic state influences the physiological activities (see Child, 1924), that I feel there is no necessity to emphasize the point further.

One may question the symmetry analogy because of the fixed position of most cells in the multicellular organism compared to the free movement of the workers building the nest (Spencer, 1885-1886; Ferrière, 1915; Wheeler, 1928b, p. 305). Symmetry, however, is seen in the constantly moving protoplasm of a protozoan organism and Driesch (1908, p. 151) points out that the bilateral skeleton of *Echinus* larvae is secreted by wandering mesenchyme cells while the cells are moving.

Although most nests of the social insects are dead constructions, and thus are best analogized with the dead structures of organisms like the shell or bony skeleton, the army ants *(Eciton)* construct their nest of their own bodies with interior chambers for the brood and queen (Schneirla, 1933, 1938). These nests vary in external form depending upon the environment. Thus we have at least one case of a sort of symmetry of activity in the living social organism with a temporary static position of the living units. The architectural nest is simply a more permanent expression of living activity gradients and its morphological attributes enable us to detect the results of the dynamic physiological events more readily.

A radial type of symmetry may be found in numerous termite nests, the most diagrammatic being the mushroom-shaped nests of the genus *Cubitermes*. An umbrella-shaped cap surmounts a column and the adaptive function seems to be the shedding of rain from the nest (Emerson, 1938, p. 273). The principle of polyisomerism presented by Gregory (1934) also finds a counterpart in some of the nests of *Cubitermes* which are composed of a succession of caps resembling in a rough way the strobila of *Aurelia*. Many nests of social wasps also show radial symmetry and replicative sections.

Bilateral symmetry of termite nests is also found in several cases. The meridian nests of *Amitermes meridionalis* (Emerson, 1938, p. 266, 268) are precisely oriented with a longitudinal axis running north and south. These

nests seem to be adapted to present the least surface to the intense rays of the sun during the tropic midday. The intimate reactions of the workers during the building process have not been studied, but the striking correlation with ecological factors would seem to indicate a reaction gradient to external stimuli. The nest type is species specific, however and doubtless genetic factors contribute to the behavior pattern which reacts to the environment. Determination of gradients by external factors influencing the protoplasmic substrate are cited by Child (1924).

The most astonishing case of superorganismic bilaterality is seen in the nest of *Procubitermes niapuensis* (Emerson, 1938, p. 275) constructed on the trunk of a tree. Above the nest proper the termites build a series of chevron-shaped ridges which shed the rain water descending the trunk, thus protecting the nest. This bilateral construction activity not only shows precise geometric pattern but, being repeated along a longitudinal axis, is suggestive of serial homology. Convergent evolution of bilateral rain-shedding ridges of a somewhat similar type is found in the nests of *Constrictotermes cavifrons* (Emerson, 1938, p. 277). In the latter case, axiate organization of the nest proper with regard to stored organic matter is also reported.

The sequence in the evolutionary development of the symmetry patterns in termite nests is not very clear, but there is no particular reason for not assuming that the sequence was from spherical through radial to bilateral types. One case, the nest of *Amitermes excellens*, even goes through a bilateral stage before becoming secondarily radial (Emerson, 1938, p. 275), thus suggesting the symmetry of the Echinodermata.

Aside from the main axiate patterns giving rise to the major types of symmetry in organisms, secondary differentials produce multitudinous cases of replicative structures, such as the tentacles of Coelenterates, which may be referred to under Gregory's term of "polyisomeres" (Gregory, 1936, p. 313). Polyisomeres may also be illustrated in termite nests, the best examples known to me being the symmetrically repeated protuberances surrounding the minute pores through the walls of nests of species of *Apicotermes* (Hegh, 1922, p. 387-389, figs. 260-262).

Much of the study of symmetry patterns in the organism has centered around the phenomenon of regeneration (Child, 1924; Andrews, 1935) and this may also be observed in the social organism. Hingston (1932, p. 306) experimentally destroyed the bilateral rain-shedding ridges above the nest of *Constrictotermes cavifrons* and eight out of eighteen ridges originally destroyed were rebuilt over a period of six weeks.

It is fairly clear that symmetry characteristic of a phylum is in some way more fundamental than symmetry characteristic only of a species or genus. It is to be assumed that the bilateral symmetry mechanism of a flatworm is far more complex than the mechanism producing a bilateral nest of a single species of termite whose close relatives may not exhibit such symmetry. Although both are clearly influenced by hereditary as well as environmental factors, the hereditary basis in one case is so complex that radical variation

among the species and genera is not found. This difference is possibly partially explained by the differential in the time that selection has operated on the complex hereditary factors through their relative functional importance. In other words, there is little doubt that the functional significance of the symmetry of a termite nest is far less than that of the flatworm, with consequent greater variability and less complexity of germinal factors.

Chemical Integration

An active field of investigation in recent years is that of transportative or chemical integration within the organism. If one kidney is removed, the other enlarges. The epidermis of Amphibia produces an eye lens if it is close to the optic vesicles, either under normal conditions or under experimental transplantation. Mammary glands can be induced to grow in a young male guinea pig if injected with ovarian hormones. Lactation can be induced if the experimental animal is injected with hypophysial extracts. The embryologists have made terms such as "organizer" (Spemann, 1925) and "embryological induction" common in biological language. The term "hormone" has been applied to a number of chemical agents which differ in certain important physiological characteristics. Some are formed in the endocrine glands and are transported by means of the blood stream. Others pass more slowly from cell to cell, or through interstices between the cells, and their effects are likely to be more local. These agents seem to be parts of enzyme systems. In the case of certain vitamines the molecule is incorporated into a more complex molecule before it is activated and doubtless complex chains of chemical reaction take place in many other cases.

Chemical agents have recently been demonstrated by Castle (1934a, p. 314; 1934b) and Light, Hartman and O. H. Emerson (MS) to be correlated with the caste differentiation in termites. Reproductives, soldiers and nymphs at various stages of development were placed in experimental colonies. If the queen were removed from a group of 50 nymphs, a new supplementary queen developed in a period from 35 to 50 days (also see Jucci, 1924). If the king were removed, a new king developed in a like period. Soldiers also were developed in greater numbers if the original soldiers were removed. The theory that these castes produced chemical exudate substances which were passed throughout the colony by means of grooming and licking was indicated by making alcohol or ether extracts from the various castes, feeding these on filter paper to the experimental colonies, and recording a definite effect upon the time of development of the respective castes. These chemical agents thus seem to inhibit the development of more individuals of the caste which produces them, but if removed or reduced, the nymphs are not then inhibited from developing and replacing the caste type. Unpublished experiments by E. M. Miller tend to show that the experimental colonies with undifferentiated nymphs end up with approximately the same proportions of the castes, regardless of the proportions at the beginning.

Wheeler (1918) proposed his theory of "trophallaxis" or exchange of nourishment as a mechanism of mutual interrelation within the colony. Many

larvae as well as adults have glandular secretions which induce social activity (Wheeler, 1918; Rau, 1928). These glands may be rather generally distributed over the surface of the insect or may be localized in the so called "exudatoria." In addition, regurgitated or glandular droplets are passed from individual to individual. The glandular royal jelly fed the developing honey bee queen and the bee bread fed the developing worker differ in chemical constitution (Wheeler, 1923, p. 138; Imms, 1931, p. 49). Anal droplets are also often eaten by other members of the colony. The termite queen exudes a clear fluid with the eggs (Emerson, 1929). This fluid attracts workers which imbibe it and the care of the eggs may be partially explained through the induced action caused by this fluid. Although these various exudates may be nutritional, specific chemical substances (coenzymes) may also be present which, when activated, can stimulate or inhibit development and behavior (Köhler, 1922; Morland, 1930, p. 140; Imms, 1931, p. 50). Wheeler (1928b) includes chemical nourishment and stimulation, gustatory as well as olfactory, under his concept of trophallaxis.

Regulation of tissues through the mechanism of phagocytosis has been demonstrated, particularly in sponges (Wilson, 1932), in metamorphic changes from tadpole to frog, and in the destruction of erythrocytes by the mammalian liver and spleen (Carlson and Johnson, 1937, p. 104). Insect larval tissues are extensively broken down by histolysis and phagocytosis (Snodgrass, 1935, p. 395) and new tissues are developed from histoblasts which derive their nutritive substances through transportation in the vascular system from phagocytized disintegrated tissues (Carpenter, 1921, p. 150). Disintegration through autolytic enzymes probably precedes phagocytosis (Smith, 1920). Surface forces are the principal factor in determining phagocytic ingestion (Mudd, McCutcheon and Lucké, 1934, p. 249).

Paralleling tissue phagocytosis the well known cannibalism among termites is probably a regulator of population density and type without loss of the nutrient materials. Cannibalism is stimulated by injury (Emerson, 1933a) and has been thought to have eugenic significance (Snell, 1932) although this latter conclusion needs verification. Cannibalism also is increased at periods when nitrogenous material is deficient (Cook and Scott, 1933, p. 104; Hendee, 1934, p. 316). The phenomenon of the elimination of excess drones in the honey bee colony has often been described, but in this case, the materials composing the bodies are wasted.

Chemical agents also seem to be the basis of colony recognition (Emerson, 1929). Not only do these agents serve to distinguish the members of a colony, but they also serve to bring about social isolation of one colony from another, a phenomenon analogous to physiological isolation and asexual reproduction in many lower invertebrates (Child, 1924). In many instances, members of one colony of social insects will be treated antagonistically if introduced into another colony of the same species. In some experiments with termites which showed such intercolonial antagonism, the individuals were first placed from 13 to 16 hours in a depopulated portion of the nest of the colony into which they were then introduced. The antagonism was eliminated by this device and

in numerous instances, introduced termites and termitophiles lived in harmony with their new associates. Victor Dropkin has performed unpublished experiments in which he placed different families of termites together *(Zootermopsis* and *Reticulitermes)* after first placing them in ethylene gas for a short time. Not only did this treatment prevent the normal antagonism between these species, but after the gas effects were deemed fully dissipated, these strange termites lived together for a number of days.

A similar colony odor relationship is also characteristic of other social insects. It may be assumed that a neutral substance on the surface of these insects absorbs the odor of the environment and that the individuals of the colony react antagonistically to any insect that does not possess the colony odor, whether the insect is of the same species or a different species. Likewise, different species may sometimes be conditioned to live together amicably through modification of the colony odor. Rau (1930) shows that *Polistes* wasps react as if there were species recognition and not colony recognition. Fielde's experiments upon ants (see Forel, 1929, p. 51) indicated reaction to nest and other local odors, inherited odor of mother, progressive odor change with age, and species odor.

We may liken these phenomena to the reactions of tissue transplants with their concomitant tissue antagonism and tissue acceptability dependent upon chemical differences and chemical similarities. Erdmann (1927) found it possible to transplant skin tissues to different species and families of Amphibia if she acclimated the donor tissues to the host medium through gradual progressive modification of the medium in tissue cultures (also see Stone, Owings and Gey, 1934). It has been fairly well demonstrated by experimental embryologists that tissues which show antagonism in older interspecific or even interclass transplantation, may be successfully transplanted in embryos or larvae (Murphy, 1914a, 1914b; Nicholas and Rudnick, 1933). Most of the transplantation experiments indicate a genetic basis for tissue acceptability or antagonism.

Nervous Integration

The most obvious coordination mechanism in the organism above the level of the plants, protozoa and sponges is the nervous system. The basic mechanism is the transmission of impulses through a chain or network of cells linking the receptor and the effector, and in the higher forms, a central nervous system with a controlling brain and subsidiary secondary centers has evolved.

Organismic sociologists have suggested analogies to the nervous system in human society with its governmental centers and its intricate system of intercommunication through telegraph, telephone and radio. Unquestionably the rapid advance of methods of communication between smaller human social units will ultimately lead to a more integrated world society (Compton, 1938), although the initial stresses of adjustment may lead to conflict.

The insect society stands at a lower level in this respect than human society. The means of precise conditioned communication by means of language and writing found in human societies is at a much more generalized

stage of development among the insects, although communication by sounds (stridulation and head hammering) are recorded (Emerson, 1929). R. Boulton (personal communication) reports that a wave of sound made by head hammering could be detected with a distinct time period of transmission when a termite colony in Angola was disturbed. Transmission of excitability by means of odors and tactile actions are reported for ants and bees (von Frisch, 1923; Allee, 1931, p. 89).

Conditioned psychic dominance, as found in many vertebrates and in man, seem to be lacking in insects (Wheeler, 1930). Leadership seems to be based upon physiological dominance (Chen, 1937b), although psychic and physiological dominance may be difficult to separate when all gradations are considered (Child, 1924).

Rhythmic Periodicity

So far I have talked primarily about the complicated interactions which are known to produce a dynamic equilibrium in the organism and superorganism. Although a relative equilibrium is reached, the organism, as well as the superorganism, exhibits cyclic behavior through variations in the mechanisms of integration. Periodicity in certain instances seems to have a definite function so that we may expect that mechanisms for producing cycles have actually been selected because of their functional value.

Environmental rhythms and the reaction of organisms to them have long been an object of study. Biologists have also been aware of internal rhythms, particularly in the reproductive and life cycles. It has become apparent in recent years that environmental factors predominate in stimulating the rhythmic response in some cases while organismic factors predominate in other instances (O. Park, 1935; Moore, et al, 1934; Wells, 1935; Huntington, 1938; Elton, 1924, 1927; Child, 1915; Carrel, 1930).

Diurnal Rhythms:—Daily rhythms of insect social activity are apparent. Most of these insects are diurnal, but the predatory activity of the ponerine ants *(Termitopone)* which raid termite colonies is largely crepuscular (Wheeler, 1936). Nocturnal activity of the leaf-cutting ants *(Atta)* is greater than in the day time, and nocturnal flight of light-colored termites is commonly observed, even though most of the termites fly in the day time and are dark colored.

The correlation between the environmental cycle and the organismic and superorganismic activity might be considered as a cause and effect relationship (O. Park and Keller, 1932), but the internal drives of hunger and sex, which in turn are determined by nervous and chemical integration mechanisms, must play an important rôle in some cases (O. Park and Sejba, 1935).

Sexual and Seasonal Rhythms:—Schneirla (1938) has given an interesting analysis of the rhythmic activity of army ants *(Eciton)* in which he postulates that the brood cycle controls the nomadic—stationary periodicity. The queen produces large numbers of eggs at intervals of approximately 36 days. The activity of the moving larvae excite the workers and this excitement increases

progressively throughout the colony through interindividual stimulation. Any stimulation which increases general excitement will augment raiding. Three or more extensively developed raiding systems during each day of this period inevitably lead to a colony migration in the afternoon. When the brood has become enclosed in cocoons, the colony becomes stationary and remains in this condition for many days during which only a single raiding system is developed each day and migration ceases. The moving pupae within the cocoons excite the workers which open the cocoons. The restless movements of the callows excite the workers tactually and perhaps chemically. The level of raiding activity is raised and daily migration is resumed. The day-night rhythm is based mainly upon excitation of light. It is thus shown that factors arising within the colony are basic in determining the army ant behavior pattern, and that factors external to the colony impart to this phenomenon the temporal and other special characteristics. The brood cycle among honey bees is postulated as an influence upon subsequent swarming by Rösch (see Morland, 1930; Imms, 1931, p. 53).

The colonizing flight of termites is an interesting example of the superorganismic parallel to the cyclic sexual activity of the organism. The production of numbers of alates in the termite colony is a periodic phenomenon. The mechanism is not fully understood, but in view of the knowledge of caste determination through chemical agents which Light and his colleagues are establishing, a fair guess may be made. If the reproductives are surrounded by a small number of offspring as in a young colony, their inhibiting "hormones" prevent any nymphs from developing into functional reproductives. It is well known that young colonists do not produce winged forms (Heath, 1931; Kalshoven, 1930). As the colony increases in numbers, the inhibiting influence of the royal pair must become lessened per individual, thus allowing some of the nymphs to develop into reproductives. Pickens (1932) suggests that the nymphs farthest from the royal pair may becomes alates. As these are stimulated to leave the nest in the colonizing flight, the decreased population is once more under the inhibitory influence of the "hormones" and no further production of alates can occur until the population has increased. Colonies under artificial conditions with spatial limitations to increase do not produce alates, even though very old. One confined colony of *Neotermes castaneus* under observation for 24 years did not produce an alate. Seasonal influences may affect the proportional amount of "hormones" or the effective threshold. Although this mechanism for the periodic production of alate termites must be experimentally verified, it is a hypothesis which fits the known facts. There is a general parallel to the hormone mechanism controlling periodic ovulation in certain mammals, which, however, involves a more complex interrelation between several stimulating and inhibiting hormones (Marshall, 1936).

The intricate mechanism of the colonizing flight is yet rather poorly understood. With certain species of termites *(Reticulitermes* and *Coptotermes),* enough study has been made to at least give us a hint of some contributing mechanisms. We know that the flight in the higher termites is correlated with the beginning of the rainy season, and often immediately follows a shower. A photopositive orientation during the time of emergence and early flight prob-

ably explains the movement from the dark to the light. A geonegative response places the alate in a better position to take flight. A certain length of time of flight in the air seems to induce the shedding of the wings. Volatile chemical emissions from the female seem to be the primary means of attracting the male (Emerson, 1929). A symmetrical tactile response operates to cause the female to move and the male to follow in tandem (Emerson, 1933b). The female moves toward a region of high humidity, loses the positive reaction to light, and together the male and female excavate a cell in the earth or in a decaying log and seal the cell from the outside. Copulation occurs after the pair are enclosed. Unquestionably this outline of events and mechanisms has gaps, and variations occur in various termites, notably in the more primitive species (Kalshoven, 1930). However, a remarkable sequence of definitive activity is certainly present which roughly parallels the orientation, movements and fertilization mechanism of the gametes of plants and animals.

Obviously this colonizing behavior is closely parallel and is a direct outgrowth of interindividual sex attraction. However, the workers definitely contribute to the flight. They make the openings in the nest through which the alates emerge, and plug them up after the flight is over. They may, on occasion, build platforms to facilitate the takeoff of the alates (Emerson, 1938, p. 257). The soldiers also guard the openings in the nest during emergence of the alates and during the preparatory labors of the workers. The parallel, of course, is to be found in the activities of the somatic tissues and organs which contribute to the discharge of the gametes of the multicellular organism.

Extrinsic factors are also obviously correlated with organismic and superorganismic seasonal periodicities. Marshall (1936, p. 449) states, "in all the higher animals sexual periodicity, while conditioned by the environment, is regulated in its successive phases by the combined integrative action of the nervous and endocrine systems."

Life Cycle:—Organismic periodicity transcending daily and seasonal cycles is seen in the phenomena of senescence and rejuvenescence (Child, 1915, 1916). The mechanisms which bring about these phases in the life cycle are actively engaging the attention of many biologists, but it is still difficult to draw many general conclusions, and we doubtless have enormous gaps in our knowledge of the dynamics of these phenomena. Not knowing the dynamics, parallelisms between the organism and the superorganism are little more than descriptive.

Bodenheimer (1937) has reviewed the data for the social insects and concludes that the growth of colonies of all social insects may be divided into three main periods: (1) the initial period of colony foundation, (2) the period of expansion and vigor, (3) the period of senescence and death. He states, "The growth of these colonies resembles that of organisms." It is obvious that the superorganismic individuality is greater than the life of the sterile individuals and, in certain cases, the reproductive individuals composing it.

Child (1916) associates senescence and rejuvenescence with metabolic

cycles. Carrel (1930) summarizes some of the principles derived from the study of cells in tissue culture. As long as waste products are eliminated and food material is supplied, fibroblasts or epithelial cells synthesize new protoplasm from the constituents of their medium. The proliferative capacity always remains present, even in old age, if the quality and quantity of the food material is correct. The innate properties of the various cell types account for the specific response of the tissue within the organism toward a given nutrient substance. The inhibitory effect of the plasma increases progressively with the age of the animal that supplies the blood. Inhibition is not due to proteins, but lipoids that can be extracted from plasma possess a very marked inhibiting effect on the growth of fibroblasts. However, the substances inhibiting fibroblasts and epithelial cells do not prevent multiplication of macrophages.

I see little indication of superorganismic accumulation of waste products (see T. Park and Woollcott, 1937). There is probably a dynamic interrelation between the mass and the peripheral functions of nutrition and protection, which would ultimately tend to equilibrate the population. The relation between spatial factors and numbers of population may limit the size and metabolism of the superorganism. Spatial extension may be limited by the efficiency and the time element of transportation within the society. It is difficult to see much indication that termite populations are limited in nature by food scarcity, but efficiency of food acquisition and transport per individual would probably reach an optimum and might pass beyond the optimum, thus bringing about a decline in population. Hjort (1938, p. 186) shows that the number of whales caught per catcher off the coast of Spain and Portugal abruptly declined while the total catch increased for two years before showing a decline. The senescence of important individual components, particularly of the reproductive castes, which sometimes occurs without replacement, would reduce the population of the whole colony. Chemical regulators may initiate forces of inhibition at certain points in the metabolic cycle. Physiological isolation parallel to that found in multicellular organisms may bring about independence of reproductive units or may result in a budding of the colony as we find in the colonizing activity of the honey bee, the army ants, and probably among termites, with a consequent rejuvenescence of the new superorganism in a new environment.

The fact is fairly clear that ontogenetic development, growth, and death, as well as sexual and asexual reproduction, are remarkably parallel in the organism and the superorganism.

Wheeler (1928a, p. 37) states that human society does not possess an ontogenetic cycle except through colonization, which he compares to the swarming of the honey bee. I should be inclined to view "budding" (Wheeler, 1933, p. 3) as well as sexual reproduction of the superorganism, as indications of an ontogenetic cycle, although one is less sharp than the other. Both involve degrees of physiological isolation, reorganization and development. Social insect colonies show a greater degree of isolation than human communities. Because of the integration between communities, human society

is as extensive as the species, while insect society extends little beyond the colony. Great cycles in human society are postulated by Spengler who speaks of the rise and fall of civilization types, a generalization which I feel incompetent to judge (see Fisher, 1930, p. 178). A great many fluctuations in human community populations have been shown to be correlated with exploitation of new resources and also with greater efficiency in social integration (Hjort, 1938).

Superorganismic Phylogeny

A study of ontogenetic development of the social organism gives us an insight into the contributing factors, but phylogeny may also furnish important evidence for organismic dynamics. Wheeler (1911, p. 313) refers to the independent activity of the reproductives during the founding of the new colony as an example of recapitulation. The significant ontogenetic and phylogenetic correlations depend upon the protoplasmic substrate which passes from generation to generation. Hereditary phenomena have been shown to be correlated almost wholly with the chromosomes (Irwin and Cole, 1936), and further analysis has often shown the correlation to be with the gene. The gene complex not only seems to be the basic element in evolution, but is precisely distributed by mitotic division to each cell unit in the organism. Ontogenetic and phylogenetic homologies would seem to rest upon a common gene arrangement.

Much as we trace taxonomic homologies in the soma of individual multicellular organisms, we can show taxonomic homologies of the sterile castes. Homology may be applied also to the activities of the sterile castes through their nest structures (Emerson, 1938) and other behavior patterns. Fungus-growing behavior of the workers is characteristic of a single subfamily of termites and a single tribe of ants. The complicated social behavior patterns possessed by different species, genera, and higher groups indicates that these behavior characteristics are hereditarily induced and their evolution probably rests upon the same sort of mechanisms producing structural divergence (Maidl, 1933-34; Gregory, 1936, p. 311).

The origin of biological adaptation is usually thought to be due to the selective action of the environment upon the results of germinal variation. The germ plasm producing a modification is selected or eliminated through the survival of the individual. Selection thus acts upon the organismic unit and not merely upon the germ plasm.

Darwin (1859) stated that the case of neuter insects was by far the most serious special difficulty which his theory of natural selection had encountered. As Darwin recognized, selection could not be acting upon the individual soldier or worker, because they were sterile and could not pass on their characteristics to any other individuals. The germ plasm of the reproductives could only be selected through the forces acting upon the colony as a whole. Weismann (1893), arguing from evidence from worker and soldier ants, concluded that "the whole colony behaves as a single animal; the state is selected, not the single individuals; and the various forms behave exactly like the parts of one individual in the course of ordinary selection." Fisher (1930, p. 182) makes the same general assumption, but also shows that an intracommunal

selection must occur in societies practising individualistic reproduction. Sturtevant (1938, p. 75) shows that selection may act upon the individual, the colony, or a population of colonies.

Marshall (1936, p. 446) draws the conclusion that the various extrinsic and intrinsic sex adjustments owe their evolution to natural selection of the sexual pair, and not to individual sexual selection as postulated by Darwin. Mechanisms of family integration, for example, the mammary glands of mammals, would seem more obviously to rest upon natural selection of the group including parents and offspring.

There is no doubt that the social life of termites, wasps, bees, ants, and man is profoundly influenced by the phylogeny through sex and family levels (Buttel-Reepen, 1915; Wheeler, 1930, 1933). There seems to have been a gradual shift from sexual to familial adjustment and from dependence of offspring upon parents to dependence of parents upon offspring. It is also obvious that other integrative mechanisms are involved. Allee (1931) has made a thorough summary of these mechanisms of group integration at non-sexual levels. There is no reason for not assuming convergent evolution of coordination in many cases, but one may also homologize the mechanisms in certain phylogenetic series.

Thus we find that the important ecological principle of natural selection acts upon the integrated organism, superorganism or population. Wright (1932, p. 365) says, "In this dependence on balance the species is like a living organism." (Also see Wright, 1937, p. 319)

If the superorganismic analogy be correct, adaptive evolution must take place without any mechanism for the inheritance of acquired characters. Darwin (1859) recognized this principle when he stated, "peculiar habits confined to the workers or sterile females, however long they might be followed, could not possibly affect the males and fertile females, which alone leave descendants." We may say, then, with considerable surety, as Weismann (1893) has already stated, that adaptive evolution does not necessitate a mechanism for the inheritance of acquired somatic characters. Our statement, however, is justified by the dynamics of the superorganism more than by what we know of the dynamics of the organism. (See Eldridge, 1925, p. 157, for an opposing view, and Emerson, 1938, for an amplified discussion)

Convergent adaptation to environmental factors can be shown within the major groups of social insects. Convergence is also quite apparent in superorganismic integration. Ants and termites form a classical example of societal convergence (Natzmer, 1915), and convergence is almost as strongly indicated in the wasps, bees and ants (Wheeler, 1928b, p. 302). A point worthy of some emphasis, because it has sometimes been ignored by physiologists, ecologists and evolutionists, is that adaptations of one unit to another unit within the organism or superorganism rests upon the same phylogenetic basis as adaptations of the whole organism or superorganism to its external environment (Ritter, 1919, p. 183).

Other phylogenetic tendencies show a parallel between the organism and

superorganism. The mechanism of degenerative evolution has recently been discussed by Wright (1929) and Emerson (1938). Degenerative evolution of the soldier caste has occurred in the genus *Anoplotermes*, and all the sterile castes have been eliminated in two species of *Vespa*, in the bee genus *Psithyrus*, and in a number of genera of ants *(Wheeleriella, Anergates)*, etc. (See Wheeler, 1923; Fisher, 1930, p. 252; Imms, 1931, p. 83). We may consider degenerative loss of the sterile castes as a parallel to the loss of many somatic tissues in the parasitic crustacean, *Sacculina*.

Carrel (1930, p. 217) seems to find difficulty in relating the plurality of the unit cells of the body with the obvious unity of the whole. He states (p. 209), "we may reasonably assume that the purposeful factors reside within the units themselves, and not within the organism as a whole." Other biologists studying other holistic levels, such as integrated populations, frequently arrive at mystical teleological explanations. It seems to me that the unity of the whole (internal adaptation) can be understood only through the perspective of genetic and evolutionary principles combined with the study of function and integration of the parts (Cannon, 1930, p. 239; Hjort, 1938, p. 43). The teleological problem can be at least partially resolved (see Hjort, 1938, p. 122) by the guiding principle of natural selection (Smuts, 1926, p. 343), without recourse to mystical "cosmic mind," "entelechy," or "superperson" (see Lighthall, 1930).

Emergent properties are characteristic of new associations. There is no doubt that evolutionary development of societies has given birth to new characteristics. Cooperative integration of newly associated parts may prove to be biologically valuable. Whitehead (1925, p. 296) says, "Those organisms are successful which modify their environments so as to assist each other." Social organisms seem to have been most successful from this standpoint.

Discussion

I think that the foregoing discussion amply demonstrates that from both ontogenetic and phylogenetic considerations, the social organism, at least as evidenced in insect societies, parallels the integrative dynamics of the organism at lower levels of individuality and at the same time, through a more complex coordination, tends to bring the environment of the organism under control, much as the multicellular organism brings the environment of the cell under control. It may be that more exact knowledge of the mechanisms and functions will show that some of the forces producing the analogies are not similar and categories applicable in a given realm may not be stretched beyond that realm (Cohen, 1931, p. 291). It should also be emphasized that, valid as the superorganismic concept may be as applied to insect societies, other principles may also be applied to societal organizations which will help us better to understand these phenomena.

The application of the concept to human society is beyond the competence of the speaker. In certain respects, the comparison seems valid, but in others which rest upon "social heredity" as compared to germinal heredity, striking differences occur which may be too great to make their analogy significant. I

feel, however, that biologists and sociologists need to study comparable facts critically in the light of new discoveries, and in numerous cases, what may seem superficial analogy may be shown to be due to fundamentally similar causal factors. "Social heredity" bears certain similarities to germinal heredity and may in part be under the influence of a sort of natural selection (Fisher, 1930, p. 183). Social integration in human society shows certain similarities to social integration in insect societies. These similarities, as well as differences, should be studied as scientifically as any of the more physiological integrating mechanisms of the organism.

It might be of interest to see what level of organismic evolution the highest insect colony has reached. The lack of clearly defined social organs, controlling social brain, and permanent symmetry patterns for large taxonomic categories, would indicate a relatively low level of organization. Our best parallels seem to be with organismic characters not far above the colonial protozoa, sponges (see Wilson, 1932), or coelenterates, and many of our analogies are hardly above the level of a unicellular organism. Much of the criticism of the superorganismic concept rests upon the difficulties of finding convincing analogies with the highest organisms.

In some ways the human social groups seem above the level of the social insects and in other ways the social insects seem to have attained a higher integration. Human social institutions may almost be thought of as social organs, but the germinal basis of society among the insects implies a longer evolutionary history and greater stability, efficiency, and coordination. Chen (1937a, p. 435) concludes, "The social increment in man and other animals is never so great as that of ants. ** The very large social increment in ants is probably due to the fact that ants are much more highly socialized than men, hens, rats, and goldfishes; hence they are much more affected by being isolated or grouped." The failure of human society to evolve a more complete specialization of reproductive and somatic functions makes the organismic analogy less convincing than in the case of the insect society.

Human social groups are able to adjust to a complex environment with greater facility and versatility, particularly through cultural or "social hereditary" mechanisms (Conn, 1914; Wheeler, 1930) combined with intricate learned behavior. Insect society works more smoothly, with less social friction and with less drag from poorly integrated elements.

The concept of the insect superorganismic individual not only rests upon the significant correlation of much factual evidence, but can definitely contribute to the formulation of a number of important biological principles. Of course, much of our evidence rests upon the use of analogy. Some biologists have tended to assume that analogy and superficiality are intimately wedded. Bowne has referred to Spencer's confusion of logical classification with genetic order as the "fallacy of the universal" (Bristol, 1915, p. 39). I hardly think it necessary to argue the importance of analogy before a group of ecologists. Much of our technique in discovering the nature of the influence of fundamental environmental factors upon biological systems rests upon the discovery of analogies. What homology is to the geneticist, analogy is to the ecologist.

One must understand analogy to detect homology and *vice versa*. Convergent adaptive evolution is only one great concept resting upon the use of analogy. It is my own opinion that an understanding of the forces which produce analogy are as scientifically profitable as an understanding of the forces producing homology (see Hjort, 1938, p. 101). Natural Selection often results in the evolution of similar functions determined in part by quite different and therefore analogous mechanisms (Lillie, F. R. 1938, p. 71). We thus have evidence to indicate that function may dominate the mechanism, even without recourse to mystical teleology. Wright (1935, p. 370), referring to Karl Pearson's view, says, "science is always essentially statistical, being always based on classifications which of necessity throw more or less diverse things into common categories." However, one must have detailed objective evidence, when using analogical method, that the environmental forces have identity, much as the concept of homology demands an identity of genetic and developmental forces. The existence of significant analogy should stimulate us to an increased study of causative factors (Fisher, 1930, p. 179).

I shall do no more than mention the remarkable parallelism between the intraspecific or homotypic superorganism and the interspecific or heterotypic ecological community. Others in this series of discussions have dealt with what might be called the interspecific superorganism.

Cleveland (1934, p. 209) points out that colony life in the more primitive termites is essential since the cellulose digesting protozoa are lost at each molt and reinfection can only take place through association with non-molting individuals. In the case of the roach, *Cryptocercus*, however, transmission of protozoa only occurs at the time of molting so that the recently hatched roach must live with molting nymphs. New colonies could not be started by adult pairs of roaches, therefore, while new colonies of termites can be founded by a pair carrying protozoa. We thus see how interspecific symbiotic relations may determine major patterns of family and social life among these insects.

The symbiotic protozoa and termitophilous and myrmecophilous insects, together with the scavengers, predators, parasites, nest eaters, and inquilines, show varying degrees of integration with the higher social insects. Many of these interspecific associations depend upon the evolution of societies, particularly the slave makers and social parasites (Imms, 1931, p. 83; Fisher, 1930, p. 252), as well as the symphiles among ant and termite guests. The same forces which bring about the integration of the organismic units within the species can also be shown to be active in the ecological community which, of course, came into existence not long after the origin of life itself. The organism, in a sense, projects itself into the community because so many species in the community are adjusted to special organismic structures and integrative mechanisms. The ecological community also has an ontogeny (succession) and a phylogeny. One might question the phylogeny of the ecological community on the basis of the lack of germinal continuity of the unit, but we must remember that individual genes and chromosomes show independent assortment in the history and dynamics of the germ plasm, and thus parallel the independent assortment of germ plasms among the species composing the

integrated ecological community. The ecological community may exhibit loosely integrated components, but such closely integrated relationships as the cellulose-digesting symbiotic flagellates with their roach and termite hosts have a long history indicating greater stability than the "ageless" mountains.

Possibly we should classify ecological associations as ascending levels of super-superorganismic integration which show partial physiological isolation between the community types, and complete isolation only between the biota of this planet and that of some other planet. The integration of all life on the earth forms a "Leviathan," to use Patten's (1920) term, and the analysis and synthesis of the mechanisms of this "Leviathan" are the major duty of the ecologist. Let us not, however, raise the superorganismic concept to an all or none principle. Let us rather use the perspective it gives us to stimulate further study and understanding.

REFERENCES

ALLEE, W. C. 1931—Animal Aggregations. Univer. Chicago Press, Chicago.

ALVERDES, F. 1927—Social Life in the Animal World. Harcourt Brace & Co., N. Y.

———1932—The Psychology of Animals. Harcourt Brace & Co., N. Y.

———1937—Kausalität, Finalität und Ganzheit. Acta Biotheoretica **3**(3):167-180.

ANDREWS, E. A. 1935—Shell repair by the snail, *Neritina*. Jour. Exp. Zool. **70**: 75-107.

BODENHEIMER, F. S. 1937—Population problems of social insects. Biol. Rev. **12**:393-430.

BRISTOL, L. M. 1915—Social Adaptation. Cambridge, Mass.

BROWN, H. C. 1926—A Materialist's View of the Concept of Levels. Jour. Philos. **23**:113-120.

BUTTEL-REEPEN, H. v. 1915—Leben und Wesen der Bienen. Braunschweig.

CANNON, W. B. 1930—The integrative action of the vascular system. Chapt. X in Cowdry, E. V. Human Biology and racial welfare. Hoeber, N. Y.

CARLSON, ANTON, AND VICTOR JOHNSON. 1937—The machinery of the body. Univ. Chicago Press, Chicago. 580 pp.

CARPENTER, G. H. 1921—Insect Transformation. Methuen & Co. London.

CARREL, ALEXIS. 1930—The relation of cells to one another. Chapt. IX. Cowdry, E. V. Human Biology and Racial Welfare. Hoeber, N. Y.

CASTLE, GORDON B. 1934a—The experimental determination of caste differentiation in termites. Science **80**(2075):314.

———1934b—The Damp-wood termites of western United States, genus *Zootermopsis*. Cap. 24. Kofoid, C. A. et al. Termites and Termite Control. Univ. Calif. Press, Berkeley, Calif.

CHEN, SHISAN C. 1937a—Social Modification of the Activity of Ants in Nest-building. Physiol. Zool. **10**(4):420-436.

———1937b—The Leaders and Followers among the Ants in Nest-building. Physiol. Zool. **10**(4):437-455.

CHILD, C. M. 1915—Senescence and Rejuvenescence. Univ. Chicago Press, Chicago.

———1916—Age cycles and other periodicities in organisms. Proc. Amer. Philos. Soc. **55**:330-339.

———1924—Physiological foundations of behavior. Henry Holt and Company, New York.

CLEVELAND, L. R. 1934—The wood-feeding roach *Cryptocercus*, its protozoa, and the symbiosis between protozoa and roach. Mem. Amer. Acad. Arts and Sci. **17**(2):185-342.

COHEN, MORRIS R. 1931—Reason and Nature, an Essay on the Meaning of Scientific Method. Harcourt Brace & Co., N. Y. 470 pp.

COKER, F. W. 1910—Organismic theories of the state. Columbia Univ. Studies in Political Science (Studies in History, Economics and Public Law) **38**(2):1-209.

COMBES, MARGUERITE. 1937—Existence probable d'une élite non différenciée d'aspect, constituant les véritables ouviéres chez les Formica. Compt. Rend. Acad. Sci. (Paris) **204**(22):1674-1675.

COMPTON, A. H. 1938—Physics and the future. Science **88**(2275):115-121.

COMTE, AUGUSTE. 1830-42—Cours de philosophie positive. (1877. 4me ed. 6 toms. Paris.)

CONGER, G. P. 1925—The Doctrine of Levels. Jour. Philos. **22**:309-321.

CONN, H. W. 1914—Social Heredity and Social Evolution. Abingdon Press, N. Y.

COOK, S. F. AND K. G. SCOTT. 1933—The Nutritional Requirements of *Zootermopsis (Termopsis) augusticollis*. Jour. Cellular & Comp. Physiol. **4**(1):95-110.

DARWIN, C. 1859—The origin of species. John Murray, London.

DENDY, ARTHUR. 1924—The biological foundations of society. D. Appleton & Co., N. Y. 197 pp.

DRIESCH, HANS. 1908—The Science and Philosophy of the Organism. 2 vols. Adam and Charles Black, London.

ELDRIDGE, SEBA. 1925—The Organization of Life. New York.

ELTON, C. S. 1924—Periodic fluctuations in the numbers of animals: their causes and effects. Brit. Jour. Exp. Biol. **2**:119-163.

———1927—Animal Ecology. Macmillan, N. Y.

EMERSON, A. E. 1926—Development of a soldier of *Nasutitermes (Constrictotermes) cavifrons* (Holmgren) and its Phylogenetic Significance. Zoologica **7**(2):69-100.

———1929—Communication among termites. Trans. Fourth Intern. Congr. Entom. **2**:722-727.

———1933a—Conditioned behavior among termites (Isoptera). Psyche **40**:125-129.

———1933b—The mechanism of tandem behavior following the colonizing flight in termites. Anat. Rec. **57**(4) (Suppl.):61-62 (Abstract No. 78).

———1938—Termite Nests—A study of the Phylogeny of Behavior. Ecol. Monogr. **8**:247-284.

ERDMANN, RHODA. 1927—Verwandtschaftsbeziehungen der Anurenfamilien, geprüft durch Implantationsversuche gezüchteter Haut. Zeitschr. f. Wissenschaft. Biol. Abt. D. Roux' Archiv f. Entwicklungsmechanik Organ. **112**(2):739-806.

FERRIÈRE, A. 1915—La Loi du Progrès en Biologie et en Sociologie et la Question de l'Organisme Social. Giard et Briere, Paris.

FISHER, R. A. 1930—The Genetical Theory of Natural Selection. Clarendon Press, Oxford, England.

FOREL, A. 1929—The social world of the Ants. Am. ed. Albert & Charles Boni, New York. 2 vols.

FRISCH, K. VON. 1923—Ueber die "Sprache" der Bienen. G. Fischer, Jena. 186 pp.

GERSTUNG, F. 1926—Der Bien und seine Zucht. 7th ed. Berlin.

GREGG, R. E. 1938—Origin of Castes in Ants. (Review of Wheeler, 1937). Ecology **19**(2):312-314.

GREGORY, W. K. 1934—Polyisomerism and anisomerism in cranial and dental evolution among vertebrates. Proc. Nat. Acad. Sci. **20**(1):1-9.

———1936—The transformation of organic designs: A review of the origin and deployment of the earlier vertebrates. Biol. Rev. **11**:311-344.

HARE, LAURA. 1934—Caste determination and differentiation with special reference to the genus *Reticulitermes* (Isoptera). Jour. Morph. **56**:267-293.

HEATH, HAROLD. 1928—Fertile termite soldiers. Biol. Bull. **54**:324-326.

———1931—Experiments in termite caste development. Science **73**:431.

HEGH, E. 1922—Les Termite. Bruxelles. 756 pp.

HENDEE, ESTHER. 1934—The rôle of fungi in the diet of termites. Science **80**(2075): 316.

HINGSTON, R. W. G. 1932—A Naturalist in the Guiana Forest. Longmans, Green & Co., N. Y. 384 pp.

HJORT, JOHAN. 1938—The human value of biology. Harvard Univ. Press, Cambridge, Mass. 241 pp.

HOLDAWAY, F. G. 1933—The composition of different regions of mounds of *Eutermes exitiosus* Hill. Jour Counc. Sci. Ind. Res. **6**:160-165.

HOLMGREN, N. 1909—Termitenstudien. 1. Anatomische Untersuchungen. Kungl. Svenska Vet.-Akad. Handl. **44**(3):1-215.

HUNTINGTON, ELLSWORTH. 1938—Season of Birth. John Wiley and Sons, N. Y.

HUXLEY, J. S. 1912—The Individual in the Animal Kingdom. Cambr. Univ. Press, Cambridge, England.

———1927—Further work on Heterogonic Growth. Biol. Zentralbl. **47**:151-163.

IMMS, A. D. 1919—On the Structure and Biology of *Archotermopsis*, together with Descriptions of New Species of Intestinal Protozoa, and General Observations on the Isoptera. Phil. Trans. Roy Soc. London. Ser. B. **209**:75-180.

———1931—Social Behaviour in Insects. The Dial Press, N. Y.

IRWIN, M. R. AND L. J. COLE. 1936—Immunogenetic Studies of species and of species hybrids from the cross of *Columba livia* and *Streptopelia risoria*. Jour. Exp. Zool. **73**:309-318.

JUCCI, CARLO. 1924—Su la differenziazione de la caste ne la societa dei termitidi. Reale Accad. Nazion. Lincei **14** (5th ser.):267-500.

KALSHOVEN, L. G. E. 1930—De Biologie van de Djatitermiet (*Kalotermes tectonae* Damm.) in verband met zijn Bestrijding. (Bionomics of *Kalotermes tectonae* Damm. as a base for its control). 154 pp. H. Veenman & Zonen, Wageningen.

KÖHLER, A. 1922—Neue Untersuchungen über den Futtersaft der Bienen. Verh. Deutsch. Zool. Ges. **27**:105-107.

LAMEERE, AUGUSTE. 1922—The Origin of Insect Societies. Smiths. Rept. for **1920** (Publ. 2642):511-522.

———1931—La philosophie des sociétés des insects. Mém. Soc. ent. Belg. **23** (XVII-XXVIII).

LETOURNEAU, CH. 1895—The Evolution of Marriage and of the Family. Walter Scott, Ltd., London.

LIGHT, S. F., HARTMAN, OLGA, AND O. H. EMERSON.—Social Hormones in the Termite Colony. (MS).

LIGHTALL, W. D. 1930—The Person of Evolution. Macmillan, Toronto, London, N.Y.

LILLIE, F. R. 1938—Zoological Sciences in the future. Science **88**(2273):65-72.

LILLIE, R. S. 1938—The Natur of Organizing Action. Amer. Nat. **72**:389-415.

MAIDL, FRANZ. 1933-34—Die Lebensgewohnheiten und Instinkte der staatenbildenden Insekten. Fr. Wagner, Wien. 823 pp.

MANWARING, W. H. 1938—Organic Theory of the State. Sci. Monthly **47**(1):48-50.

MARSHALL, F. H. A. 1936—Sexual periodicity and the causes which determine it. Philos. Trans. Roy. Soc. London Ser. B. **226**(539):423-456.

MOORE, C. R., SIMMONS, G. F., WELLS, L. J., ZALESKY, M., AND W. O. NELSON. 1934—On the control of reproductive activity in an annual-breeding mammal. *(Citellus tridecemlineatus)*. Anat. Rec. **60**(3):279-289.

MORGAN, C. LLOYD. 1933—The Emergence of Novelty. Williams & Norgate, London.

MORLAND, D. M. T. 1930—On the causes of swarming in the honey bee *(Apis mellifica* L.*)*; an examination of the brood food theory. Ann. Appl. Biol. **17**:137-147.

MUDD, S., M. MCCUTCHEON, AND B. LUCKÉ. 1934—Phagocytosis. Physiol. Rev. **14**(2):210-275.

MURPHY, J. B. 1914a—Studies in tissue specificity. II. The ultimate fate of mammalian tissue implanted in the chick embryo. Jour. Exp. Med. **19**:181-186.

———1914b—Studies in tissue specificity. III. Factors of resistance to heteroplastic tissue-grafting. Jour. Exp. Med. **19**:513-521.

NATZMER, G. V. 1915—Über Konvergenzen im Leben der Ameisen und Termiten. Zeitschr. wiss. Insektenbiol. **11**:161-165.

NEWMAN, H. H. 1936—Outlines of General Zoology. The Macmillan Co. N. Y. 3rd ed. Chap. V. 51-61.

NICHOLAS, J. S., AND D. RUDNICK. 1933—The development of embryonic rat tissue upon the chick chorioallantois. Jour. Exp. Zool. **66**:193-261.

PARK, ORLANDO. 1935—Studies in Nocturnal Ecology. III. Recording Apparatus and Further Analysis of Activity Rhythm. Ecology **16**(2):152-163.

PARK, O. AND J. G. KELLER. 1932—Studies in Nocturnal Ecology. II. Preliminary analysis of activity rhythm in nocturnal forest insects. Ecology **13**(4):335-347.

PARK, O. AND O. SEJBA. 1935—Studies in Nocturnal Ecology. IV. *Megalodacne heros*. Ecology **16**(2):164-172.

PARK, T. AND N. WOOLCOTT. 1937—Studies in Population Physiology. VII. The Relation of Environmental Coonditioning to the Decline of *Tribolium confusum* Populations. Physiol. Zool. **10**:197-211.

PATTEN, WM. 1920—The Grand Strategy of Evolution (The social philosophy of a biologist). Badger, Boston. 430 pp.

PEPPER, STEPHEN C. 1926—Emergence. Jour. Philos. **23**:241-245.

PICKENS, A. L. 1932—Observations on the genus *Reticulitermes* Holmgren. Pan-Pacific Ent. **8**:178-180.

RABAUD, ÉTIENNE. 1937—Phénomène social et sociétés animales. Alcan, Paris. 321 pp.

RAU, PHIL. 1928—Trophallaxis in *Polistes pallipes*. Psyche **35**(3):153-156.

———1930—Animosity and tolerance in several species of *Polistes* wasps. Jour. Comp. Psychol. **10**(3):267-286.

RITTER, W. E. 1919—The Unity of the Organism. R. G. Badger, Boston. 2 vols.

RÖSCH, G. A. 1925—Untersuchungen über die Arbeitsteilung im Bienenstaat. Part I. Zeitschr. f. vergl. Physiol. **2**:571-631.

———1927—Untersuchungen über die Arbeitsteilung im Bienenstaat. Part II. Das Alter der Baubienen. Zeitschr. f. vergl. Physiol. **6**:264-98.

SCHMIEDER, R. G. 1938—(Review) Mosaics and other anomalies among ants. W. M. Wheeler. Ent. News **49**(7):208-209.

SCHNEIRLA, T. C. 1933—Studies on Army Ants in Panama. Jour. Comp. Psychol. **15**(2):267-299.

———1938—A Theory of Army-ant behavior based upon the analysis of activities in a representative species. Jour. Comp. Psychol. **25**(1):51-90.

SMITH, LOUISE. 1920—The hyobranchial apparatus of *Spelerpes bislineatus*. Jour. Morph. **33**:542-549.

SMUTS, J. C. 1926—Holism and Evolution. London & New York.

SNELL, G. D. 1932—The rôle of male parthenogenesis in the evolution of the social Hymenoptera. Amer. Nat. **66**:381-384.

———1935—The determination of sex in *Habrobracon*. Proc. Nat. Acad. Sci. **21**:446-453.

SNODGRASS, R. E. 1935—Principles of Insect Morphology. McGraw-Hill, New York.

SNYDER, T. E. 1924—"Adaptations" to Social Life: The Termites (Isoptera). Smiths. Misc. Coll. **76**(12):1-14.

———1926—The Biology of the termite castes. Quart. Rev. Biol. **1**(4):522-552.

SPEMANN, H. 1925—Some factors of animal development. Brit. Jour. Exp. Biol. **2**:493-504.

SPENCER, HERBERT. 1860—The social organism. Westminster Rev. **73**:90-121.

———1885-1886—The Principles of Sociology. (1876-80. 3rd ed. 3 vols.) New York.

STONE, H. B., OWINGS, J. C., AND G. O. GEY. 1934—Transplantation of living grafts of thyroid and parathyroid glands. Ann. Surg. **100**:613-628.

STURTEVANT, A. N. 1938—Essays on Evolution. II. On the effects of selection on Social Insects. Quart. Rev. Biol. **13**(1):74-76.

SUMNER, W. G. AND A. G. KELLER. 1927—The Science of Society. 4 vols. Yale Univ. Press, New Haven.

THOMPSON, C. B. 1917—Origin of the Castes of the Common Termite, *Leucotermes flavipes* Kol. Jour. Morph. **30**:83-153.

———1919—The development of the castes of nine genera and thirteen species of termites. Biol. Bull. **36**:379-398.

———1922—The castes of *Termopsis*. Jour. Morph. **36**:495-535.

WEISMANN, A. 1893—The all-sufficiency of Natural Selection. Contemporary Review **64**:309-338, 596-610.

WELLS, L. J. 1935—Seasonal sexual rhythm and its experimental modification in the male of the thirteen-lined ground squirrel *(Citellus tridecemlineatus)*. Anat. Rec. **62**:409-447.

WHEELER, W. M. 1911—The Ant colony as an organism. Jour. Morph. **22**:307-325.

———1918—A study of some ant larvae, with a consideration of the origin and meaning of the social habit among insects. Proc. Amer. Philos. Soc. **57**:293-343.

———1923—Social Life Among the Insects. Harcourt Brace & Co., N. Y.

———1928a—Emergent Evolution and the development of societies. W. W. Norton & Co., N. Y. 80 pp.

———1928b—Insect Societies, their Origin and Evolution. Keegan Paul, London.

———1930—Societal Evolution. Chap. VI in Cowdry, E. V. Human Biology and racial welfare. Paul B. Hoeber, New York.

———1933—Colony-Founding Among Ants. Harvard Univ. Press, Combridge, Mass. 179 pp.

———1936—Ecological relations of Ponerine and other ants to termites. Proc. Amer. Acad. Arts & Sci. **71**:159-243.

———1937—Mosaics and other anomalies among ants. Harvard Univ. Press, Cambridge, Mass. 95 pp.

WHITEHEAD, A. N. 1925—Science and the Modern World. London & New York.

WHITING, P. W. 1935—Sex determination in bees and wasps. Jour. Hered. **26**(7):263-278.

———1938—Anomalies and caste determination in ants. Jour. Hered. **29**(5):189-193.

WILSON, H. V. 1932—Sponges and Biology. Amer. Nat. **66**:159-170.

WRIGHT, S. 1929—Fisher's theory of dominance. Amer. Nat. **63**:274-279.

———1932—The Roles of Mutation, Inbreeding, Crossbreeding and Selection in Evolution. Proc. 6th Internat. Congr. Genetics **1**:356-366.

———1934—Genetics of Abnormal Growth in the Guinea Pig. Cold Spring Harbor Symposia on Quantitative Biology **2**:137-147.

———1935—The Emergence of Novelty. (Review of Morgan, C. L. 1933.) Jour. Hered. **26**(9):369-373.

———1937—The distribution of gene frequencies in populations. Proc. Nat. Acad. Sci. **23**:307-320.

DEPARTMENT OF ZOOLOGY,
THE UNIVERSITY OF CHICAGO,
CHICAGO, ILL.

DISCUSSION

Tinbergen: I like the speaker's points of view so much that it will be impossible for me to give any criticism. But I should like to add a few facts that were not stressed and which I know from the literature rather than from personal experience. In the honey bee division of labor between the different groups of honey and pollen collectors is known. One group works on a special flower and the individuals of that group work only on that flower. When that species of flower ceases to give food all the bees belonging to that group remain in the hive until some few individuals fly out again in an attempt to find a new plant or a new species. As soon as they have found a new plant they come back to the hive for a honey dance and by their dance the odor of the new flower is communicated to the waiting group. I do not know whether a structural difference between the searcher bees and the other bees will be found, but there is a functional division of labor like that between receptors and effectors, i.e., the searchers having the same function as receptors. Another example is the regulation of temperature in the bee hive. Although the individuals are cold-blooded the community as a whole has a regulatory mechanism to keep the temperature in the winter rather constant. As soon as the temperature falls below a definite limit the individuals in the outer margin will vibrate their wings and cause a rise in temperature.

Emerson: Apparently these principles are seen a little better in honey bees than in other social insects. I have witnessed a certain localized behavior in termite colonies where closely associated individuals were not involved and Chen has studied leadership in ants. I would like to emphasize the principle of organismic control of internal environment. The evolution of the multicellular organism provides more optimum conditions for all the units and better control of internal environment. I am confident that a similar evolution is taking place in the superorganism. It is true that the nest structure and many of the activities of social insects function to produce a controlled environment in which the animals are living. Termites, dependent on an almost saturated humidity, are among the common animals of the desert region because of their social control of the environment.

MacGinitie: A comparison of multicellular animals with unicellular ones reveals the apparent advantage of the former as being more efficient. Because a particular cell can do particular things, it does not need to be as specialized as the protozoan cell. The same thing is true of the superorganism; the individual in the social colony does not need to be as complex as an organism which lives without social advantages. Comparing the superorganism with a free living individual, the individual does as a single animal all that a social superorganism does as a superorganism. Consequently, the individual is better entitled to the designation superorganism because it performs as a single unit everything that the superorganism does. The botanist could give many interesting comparisons, e.g. the compass plant, the mosaic display of leaves of many plants with its great regularity of pattern.

The environment of a cell and of an organism is certainly analogous. In comparing the organization of the superorganism with other animals as far as the nervous system is concerned, I think the speaker did not avail himself of all his opportunities since the superorganism starts with a very complex nervous system. Integration of these nervous systems should give some integration of an higher order. Regarding dominance of environment many data were presented to show that the superorganism is as much a creature of its environment as a free living species. Dominance has been discussed considerably but I think that it is not in the plan of nature for any creature to become dominant except in conformity with the limits of variation. That has been expressed by thousands of writers and one of them, Dr. J. Grinnell of the University of California, in conversation with me believes that man is treading on dangerous ground because of his dominance.

Emerson: Of course, it would have been rather easy to extend these parallels further. I tried to show that the functional integration of the individual organism is repeated by the activity of populations of organisms.

MacGinitie: In my opinion, the superorganism is a social organism and as such is better than an individual organism, but it is not entitled to the term "super" since its parts are simpler than free living organisms.

Emerson: I used the term "superorganism" because this unit has evolved from a group of organisms. It is both a social organism and a group of organisms. Obviously, both principles are involved.

Park: I wish to ask the speaker two general questions: first, for a criticism of his own presentation and an indication of some of the weaknesses of the concept of superorganism. Second, turning to the field of human sociology, I think one could present this problem. If the concept of the superorganism were developed before a group of sociologists their reactions would be one of three: (a) they would not agree and couldn't be persuaded to agree to the concept; (b) they would agree and see the force of the argument, and (c) they would agree but ask, "What of it?" That "what of it" interests me and I should appreciate getting the speaker's reaction to such a viewpoint.

Emerson: One weakness in the rigid application of the organismic concept to the social insect group is the fact that the sexes are genetically heterogeneous indicating an evolution through sex groupings. I should have to know a great deal more than I know now before I would be willing to state that the superorganismic concept is a very important concept in the study of human society. However, much of the early growth of human sociology is around this concept. Plato incorporated it in his "Republic" and Thomas Aquinas was influenced by the concept. Much of the literature on the superorganismic concept relates to human sociology and only relatively recently is the concept found in the biological literature.

"What of it?" Dr. Ogburn of the department of Sociology at the University of Chicago read the paper and said, 'Suppose that you show that these integrating mechanisms are all similar; suppose you show that the units are incorporated into this structure; what do you have?' My answer, I think, justifies the concept as far as insect societies are concerned. The principle of natural selection is operating upon these units and upon other population units. The facts seem to be understood only through this theory and the theory is augmented through consideration of these facts. Does natural selection act upon inter-specific community units? Here I begin to feel certain trepidations, but I think the concept of the superorganism should be considered in the analysis and synthesis of the ecological community and at least some applications may be found to be valid. When I try to think of the relationship between one of the dominant plants of a community with one of the other members of the community in terms of biotic integration, I sense difficulties in attempting to incorporate the units into a complex superorganism. When I consider the Yucca and the Yucca Moth, however, I think certain aspects of the superorganismic concept may be of use. There is probably a gradation between highly integrated ecological units and more loosely integrated units.

Lippmaa: In view of the pronounced differences between an organism and a colony of organisms, would it not be better to refer to such specialized colonies as the termite colony as a community of organisms?

Emerson: I think it is both. Certainly, it is a community of organisms as far as the individual components are concerned. When the integrating mechanisms, however, are considered, the community possesses aspects of a single individual. That brings us back to the philosophical discussion of what we mean by the individual. An individual flat worm in the process of forming zooids asexually makes it difficult to determine just where one individual starts and ends. The bee colony during the process of swarming presents similar difficulties of definition. I am confident that the individual distinction of the superorganism among insect societies is sharper than in human societies. We do have degrees of physiological isolation separating social units in both human and insect societies. We can study the integration processes discovered in the social insects and apply our knowledge, in part at least, to studies of human society and to studies of various organismic units. Human societal evolution is probably influenced by many

illogical forces and emotional activities. Even though we understand phases of human society, our knowledge may not have a great deal of influence upon the evolution of the human society. The evolutionary forces will be operating, however, with or without human knowledge of them.

Mayr: Isn't there one rather principal difference between organism and superorganism? An organism is always an organism whether it is a highly developed vertebrate or a primitive amoeba. A social organization is not always a superorganism which is clear only in its higher forms. There is a gradual change from the highly organized insect state (superorganism) to all sorts of animal aggregations. Lower forms of social organization or aggregations can no longer be called superorganisms.

Emerson: The difficulties of delimitation are very real. I am rather inclined to the view that it might be just as difficult to determine the limits of a slime mold as an organism as it would be to delimit a colony of army ants.

Banta: I think it was implied that the integration of the individual in the superorganism of these termites is practically complete with a complete loss of individualism. In human social organizations, the individualistic tendency makes the integration less complete, although we see today in various parts of the world a suppression of individualism and a tendency toward loss of human individualism.

Emerson: I think we should immediately find parallels with the lower types of multicellular organisms. Sometimes units of organisms may carry on a certain degree of individual activity. I have not discussed all the intergradations for several reasons. Wheeler and Allee have already given us an outline of the graded series. I preferred to organize my paper around the mechanisms of integration which are often shown more clearly in the more highly specialized forms.

Noble: Frequent reference has been made to man. In the vertebrates below man we find that the most complex social organizations are found in those groups that depend largely upon vision, as for example, among the fish and birds. In some insects the visual data play a very important part in their social integration. But I was wondering if in the insects with the most complex social behavior visual cues are important.

Emerson: Termites have compound eyes, but the only use they make of the compound eyes seems to be during the colonizing flight. The sterile castes usually have vestigial eyes and live mostly in the dark. Of course, all these insects have elaborate nervous systems and much of their behavior integration is dependent upon their nervous system. However, there is no specialized sterile caste forming a superorganismic parallel to the nervous system of a multicellular animal.

On the Analysis of Social Organization among Vertebrates, with Special Reference to Birds*

N. Tinbergen

The study of social organization of animals is still in a transitory stage between purely descriptive and more causal-analytical investigation. Yet at present, we possess very few descriptions of social organization that might be called more or less complete, and the available analyses are still more fragmentary. A study of recent textbooks such as those by Alverdes (1925), Deegener (1918), and Murchison (1935) will show this. Even Allee's books (1931, 1938), while containing many analytical data, especially about the *effects* of crowding, offer an incomplete picture of social organization, as is natural in the present stage of work in this field.

It is often assumed that social relations in the higher animals are so variable, even within the species, that a general picture of social organization in a given species is impossible. Admitting the influence of individual differences on the form of social organization, I should like to point out the fact that there is always a framework of relationships that is characteristic for the species, even among the highest mammals. This has been demonstrated best by Carpenter's monograph (1934) on the Howling Monkey.

The most important work of a causal analytical character has been done on birds. Valuable contributions have been published by Heinroth (1910) on Anatidae, by Howard (1907-1915) on the old world warblers, by Verwey (1930) on the European Blue Heron, by Noble and his associates on fishes, lizards and birds, by Huxley on the Crested Grebe (1914) and on the Red throated Diver (1923), and by Lorenz (1931) on the European Jackdaw and other Corvidae. Based in part on the data of these authors, and on a wealth of new material, Lorenz (1935) offered a very suggestive analysis of social relations in birds. His work has been particularly fertile, and it will serve as the basis of the following account.

The conclusions to be presented in this paper will be substantiated by a few selected examples. These will be taken in part from the available literature, in part from unpublished work on the European Blackbird (*Turdus m. merula* L.), the Herring Gull (*Larus a. argentatus* Pontopp.), and the Three-spined Stickleback (*Gasterosteus aculeatus* L.), done in the Zoological Laboratory at Leiden.

I wish to emphasize the fact that this paper aims to point out certain *causes* that play a part in social integration. It neither presents a descriptive review of different *types* of animal communities nor does it deal with the *functions* of aggregative behavior.

* The writer wants to express his gratitude to Dr. G. K. Noble and Dr. Stanley A. Cain for their kind invitation to participate in the Conference on Plant and Animal Communities at Cold Spring Harbor, Aug. 29 to Sept. 3, 1938.

Defining sociology as the study of the relations between individuals of the same species, it is obvious that the sociology of any species offers a wealth of problems, for species without any interindividual relations probably do not exist among Vertebrates. In those species in which no flocking occurs, there exist, nevertheless, interindividual relations between, e.g., the members of a pair, and in addition often we find relations between parents and offspring, and among the young. In flocking species, especially in those species which reproduce gregariously, a complex system of relations between the members of the flock or herd exists.

The interindividual relations which form the primary aim of sociological research are always processes of one individual or group of individuals (for the sake of convenience called the *Actor*, or *A)* influencing another individual or group (the *Reactor*, or *R)*. This influence rarely is a direct one; often it is a highly complicated chain of processes: some activity of *A* is received by *R*, then, through *R's* sense organs, nervous system and effector system a special response of *R* results. As a consequence, the causal analysis of social organization has to be based on the study of individual behavior.

The complex of processes building up an interindividual relation may be divided into three phases: the activities of *A*, the means of communication proper, and the activities of *R*. They will be treated in reverse order, because this is the natural way followed in actual investigation.

The Activities of R

In order to find the causes of *R's* behavior we will have to divide it into as many elements as possible. Different elements may have different causes, and by treating them all alike rather than separately an attempt at causal analysis would be extremely difficult.

The simplest known reaction to an external stimulus, the reflex movement, rarely, if ever, constitutes the complete reaction of *R*. The activities, released by *A*, are always highly complicated. A simple example will serve to show this complexity. A shoal of socially swimming fishes makes a sudden turn as a reaction to the change in direction of one of them and swims with increased speed in the direction taken by the individual which happened to make the first change in its movements. This communal flight can be observed in any aggregating species of fish. The *increase* in speed may be a relatively simple response to a reflex; the *turning* in a special direction certainly is a spatially directed movement (orientation movement, taxis)[1]. The difference between reflex (and similar reactions) and a spatially determined movement (taxis) depends on the part played by external stimuli. In the first category external stimuli are merely *releasive*, in the second they are *directive*. A few examples may illustrate this difference.

[1] The word "taxis," in the sense in which it is used in the German literature, is preferred here to the term "tropism" because of its wider meaning (Cf. Kuehn, 1919).

When a group of *Daphnia* is swimming in well aerated water, the animals will spread irregularly in the available space. When CO_2 is added, it works as a releasing stimulus: the animals hurry to the surface. The movement is released by a chemical stimulus, but it is directed by light. If lighted from underneath, the animals will swim down. Thus what seems to be one movement can be analyzed as consisting of two components, working in succession.

A similar successive functioning of releasive and directive mechanisms is found in the foodseeking reactions of the carnivorous larvae of the freshwater beetle *Dysticus marginalis* L. The perception of chemical stimuli provided by a frog larva or some other prey urges the animal to dive to the bottom where it searches for the prey. The downward movements are entirely directed by light, and light coming from below causes the animal to "dive" to the surface. The diving cannot be released by visual stimuli, it has to be released by chemical stimulation first (unpublished observations of G. Kamerbeek and P. Nieuwdorp).

Several ground-breeding birds, such as Terns, Gulls, and Geese, have a special reaction to the situation "egg-outside-the-nest." Such a bird stretches its neck toward the egg, brings the bill behind it, and rolls it back to the nest, balancing the egg on the ventral surface of the mandibles. In this relatively simple response, a complicated mechanism of cooperating behavioral elements could be analyzed (Lorenz & Tinbergen 1938). The first phase, consisting of bringing the bill behind the egg, is an involved movement, provisionally called appetitive behavior (Craig 1918). The actual rolling movement can be divided into two components, viz., a consummatory action (Craig-Lorenz) or instinctive action (in the narrow meaning in which Lorenz uses the word, cf. Lorenz 1937) and a spatially directed component (taxis). Both elements are at work simultaneously, resulting in an apparently simple movement. The movement of the head toward the breast in the sagittal plane is the instinctive movement. Its principal properties are: 1. that it, when once released, runs its full course without requiring renewed stimulation, and 2. that its pattern cannot be changed by changing the external situation, e.g., by substituting a larger or a much heavier egg. The sideward balancing movements are spatially directed, and their pattern is continuously influenced by stimuli from the rolling egg. When a cylinder is substituted for the egg, the usual sideward movements are eliminated and no "taxis"-component can be observed. The complex nature of the egg rolling movement can be demonstrated by removing the egg after the reaction has been released. The first component continues: the head will be moved toward the breast, but the balancing movements are now absent.

A fourth instance demonstrates another method of anaysis and points to a similar mode of integration of these two components. Young Passerine birds such as thrushes, while in the nest, show "gaping" movements as a response to the food-carrying adult. During the first few days after hatching both releasive and directive stimuli are mechanical: a light tap on the nest releases reaction; stato-stimuli direct it. At about the ninth day, the reaction can be released by an optical stimulus (moving object). At first, it is still directed by the static organ, and 2 or 3 days may elapse before visual stimuli

influence its direction. Then the young no longer gape vertically, but turn their heads and necks toward the bill of the adult.

Consequently an analysis of the recognition marks that release the movements and of those that direct them toward the head of the adults, shows that the two stimulating situations are entirely different. Any object, provided is is larger than 3 mm. in diameter, moving, and above the horizontal plane of the young bird's eye, releases the gaping movement. Objects smaller than 3 mm., immobile, or those below this plane may be seen by the birds, but will not release the reaction. The head of the adult, however, *directing* the gaping movements, is recognized by the following characters: it changes the torso's outline, it is situated higher than any other part of the body, it comes closer to the young, it has a diameter of about one third of the torso and it is marked off from the torso by an indentation. The experiments that led to this conclusion are summarized in Fig. 1.

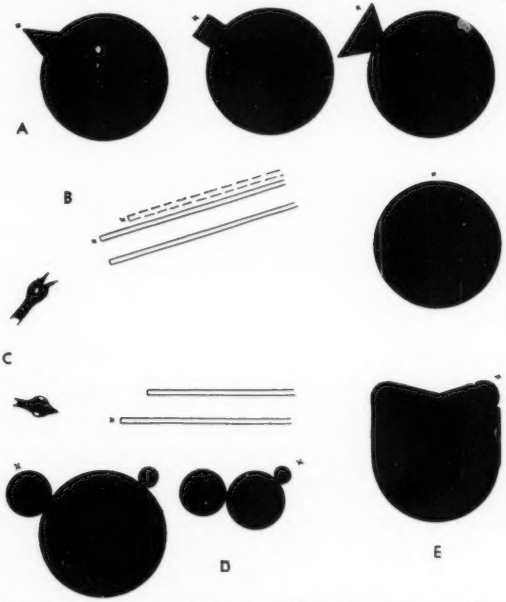


Fig. 1. A summary of experiments serving to analyze the recognition marks that *direct* the gaping movements of young thrushes to the head of the adult bird. Crosses mark the parts of the models toward which gaping is directed.
A. Changes in the torso's outline.
B. Gaping toward the highest parts of the model.
C. Gaping toward the part closest to the young.
D. Preference for one of two "heads" depends on relative size as compared with the torso rather than on absolute size.
E. The head with an indentation is preferred.

These two facts, viz., that optical stimuli may be effective as releasers of the response while still lacking any directive power, and that the optimal releasive situation differs from the optimal directive situation, indicate that in the gaping response, again, two mechanisms are at work simultaneously: a releasing and a directing mechanism (unpublished work, Tinbergen & Kuenen).

These analyses are recorded here in such detail for the purpose of emphasizing the complicated nature of an apparently "simple response." They show, that *A's* behavior may influence *R's* reactions in two fundamentally different ways.

R's readiness to respond depends on several circumstances. The endocrine condition, for instance, determines whether sexual or parental activities can be evoked at all. Apart from this, the nervous condition of *R* may vary, as the following examples may show.

In many cases *R's* readiness is not influenced by individual experience, and the innate connection between a special sense-impression and a special response remains the same throughout the period of the individual's life during which the reaction is shown. Although we have much evidence of this in lower animals its common occurrence in birds can be doubted.[2]

Many innate S-R sequences may be changed by conditioning. As an instance of a fixed, innate S-R sequence the social and sexual responses of the Guppy (*Lebiotes reticulatus* Peters) as studied by Noble (1938) may be mentioned. Noble reared Guppies in isolation and together with individuals of other species: at maturity, all of these individuals showed sexual and social responses to their own species only.

In many cases the responses are conditioned during individual life. An easy means of recognizing reactions that have been conditioned is afforded by individual differences in behavior which result from the different experiences of individuals. In social relationships, however, the conditioning occurs frequently under circumstances very much alike for all individuals. The young of those Passerine birds, for instance, that have a specialized song have to learn that song from the adults. Since all young of one species learn their song in much the same way, it is much alike. One of the most prominent characteristics of learned responses, viz. the individual differences, fails here. In many cases, therefore, the conditioning process can be discovered only by very careful observation and experiment.

Since the theories of learning are still in a chaotic state, and the knowledge of sociological facts is so fragmentary, it is impossible to present a well-classified review of the different types of learning that could be used in establishing interindividual relations. Consequently I must confine my discussion to a few individual cases, which indicate the different possibilities.

---

2 It should be noted that this applies to *sequences* between specific sense-impressions and reactions (Stimulus-Response [S-R] sequences) and not to the *pattern* of the reaction itself.

Perhaps the simplest instance of a learned reaction can be observed in places where birds of several species are breeding in close proximity to each other, as for instance in mixed colonies of Terns and Gulls. The Gulls learn to flee at the alarm-call of the Terns. In much the same way, birds of one species can learn to "understand" the threatening behavior of individuals of the other species. Black-headed Gulls, for instance, learn to avoid threatening Sandwich Terns in colonies in which both species mix.

A more complicated case is demonstrated by those birds which learn to confine their parental activities to their own young by refusing to feed or brood other young. In some species of Terns (Watson & Lashley 1915 for Sooty Terns, Dircksen 1932 for Sandwich Terns) and in the Herring Gull (Tinbergen 1936) the parent birds will feed all young of the same species they meet (provided they are of the same age as their own young) during the first few days after hatching of the eggs whereas they will direct their parental activities solely toward their own young after 3-5 days (varying according to the species). The adult Herring Gulls actually kill every strange young that happens to come onto their territory.

The establishment of rigid peck-orders (Schjelderup-Ebbe 1922 and others) involves similar learning processes. The members of a flock in which a peck-order occurs know each other individually revealing not only an amazing power of discrimination, but at the same time the working of rather intricate conditioning processes by which an animal forms separately special habits in relation to every individual.

A similar complicated relationship exists within a Herring Gullery. Every Herring Gull reacts to the alarm call of other individuals, but the pattern and the intensity of the reaction depends on which neighbors are calling. The call of neighbor *P* always causes sudden flight, whereas a similar call uttered by neighbor *Q* may result in only a slight increase in attentiveness. The animal "knows" by experience that *P* warns only when danger is near, and that *Q* often warns because of a distant disturbance.

Many birds, about to breed for the first time, return to the place where they were born. By extensive banding of birds this phenomenon has been revealed in many species. It is especially striking in the Herring Gull, a species that matures four years after birth. During these years every individual wanders widely, but at the beginning of its first reproductive season it returns to the colony in which it was born. Subsequently it returns, as a rule, year after year, not only to the same colony, but also to the same territory within that colony.

The following observations made on the Three-spined Stickleback suggest two different learning processes. The male of this strictly "territorial" species selects a locality in spring, a small part of the area in which it lives during the rest of the year, and confines its reproductive activities to it. Several activities, such as digging in the sand (the preparation of nest building) and sexual fighting are at first displayed in a rather large area. In the course of a period varying from five minutes to two hours, as the case may be, these activities are gradually restricted to a particular part of the area. The digging activities for instance include at first an area of about 20 x 40 inches, then of 15 x 30 inches, then 10 x 20 and so on, until it is ultimately confined to a spot of approximately 2 x 3 inches. In this way the depression for the nest is made.

A striking contrast to this gradual learning process is revealed by the following observation on the same species. The male, after finishing the nest, is ready to react to visiting females by piloting them to the nest. During experiments with decoys, designed to determine which "recognition-marks" of the female caused the male to guide her to the nest, a sudden change was observed in several males. After having reacted with complete piloting behavior to several decoys, lacking different recognition marks of the living female, such a male would suddenly "refuse" to respond to any decoy and would guide only optimal, living females. Without attempting further anaalysis, I wish to stress merely the difference between this learning process and that involved in the foregoing case.

Heinroth (1910) and Lorenz (1935) described a learning process that *might* differ fundamentally from other kinds of learning. A young Grey Lag Goose learns during the first *minute* of its life to direct its infant-parent-activities to the living being which it sees during this first critical encounter. If a chick hatches in the incubator and is handled by man, it will always consider man as its social companion. The only possible way to force such a chick to join adult geese, it to put it into a box or sack immediately after opening the incubator, and carry it to a Goose family with newborn chicks. Lorenz (1935) called this phenomenon "Prägung" ("imprinting") and emphasized its irreversibility; he claims that an imprinted S-P sequence cannot be "forgotten" and hence is comparable to the process of induction known in the physiology of development. Opinions regarding the nature of this process of imprinting differ of course greatly owing to the fragmentary character of the available factual material.

In many cases a change in the behavior of an individual may be due to causes other than learning processes. An innate activity does not always function at birth, but may sooner or later come into play. Flight reactions of young birds, for instance, may suddenly appear in the fledglings, and may be directed toward situations previously not flight-inducing. Sexual activities may also be entirely innate and may become apparent only after the animal has reached maturity. Many other instances could be cited. In man, many changes in behavior appearing during individual development might have an innate basis at least. The new reactions may appear gradually and pass through a slow maturation process. This maturation may concern the motor side of the reaction or it may concern the receptive side. Often it may concern both elements of the reaction. Frequently it is difficult to recognize a maturation process as such without experiment. An instructive instance can be found in the work of Noble & Vogt (1935) on sex recognition in the Redwinged Blackbird. They found that year old males apparently did not discriminate between sex in mounted specimens of the same species, and that they copulated with stuffed males as well as with stuffed females. Two year old males, however, copulated only with females. Apparently, the motor side of the reaction was fully matured, and the authors assume that the difference in discrimination between year old and two year old birds was due to conditioning of the older birds. Conclusive evidence for this opinion, however, is not presented and the possibility of a maturation process still remains.

Apart from these learning processes, summation of sense impressions may play an important part in complicating the simple stimulus response of an innate reaction. We know from many cases of courtship activities in birds, that a stimulating activity of one individual may seem to be without any effect on the partner, although after repeated performance it may elicit the partner's response. Some lasting effect of the first stimulations must be assumed.

This summation process may even have an important influence beyond the nervous system. Craig (1908) was the first to prove that sensory stimulation, derived from the courtship behavior of the sex partner, may induce both sex organs and endocrine glands in pigeons to develop. The courtship activities in these birds serve primarily to synchronize the sexual cycles of the partners, so important in regard to the specialized method of rearing the

young. The same synchronization process probably occurs in the Ruffed Grouse (Allen 1934). Recently Darling (1938) developed a hypothesis that in colony breeding species of birds a similar stimulation and synchronization of the cycles of all individuals of the colony is effected by the courtship behavior. The evidence for this assumption, however, is very meager.

Another interesting feature is the fact that the learning ability for certain situations may be dependent on the endocrine condition. I observed a striking example in young male Eskimo sledge dogs. These dogs live in packs in much the same way as do wolves in winter. Every pack has a pack territory which is defended by all members of the pack. Young males, sons of one of the pack's females, do not defend the territory as long as they are sexually immature. Nor are they aware during that period of the boundaries of strange territories, and trespass over and over again without learning that the punishment (attack by other dogs) depends on the locality. In two animals which were carefully watched during this period, defense of their own territory was assumed together with mature sexual behavior (copulation), and in the same week in which these two new reactions appeared, the dogs suddenly learned to avoid strange territories! (Unpublished observations).

Some observations seem to show that in individuals developed under natural conditions, learning processes play a rôle only in a part of the behavioral elements; some reactions are conditioned whereas others are not. Apparently in some reactions the S-R sequence functions from the very beginning while in other reactions conditioning is necessary. One could say, that for some reactions an "innate ability to be conditioned" is inherited, for others not. Lorenz first called attention to this fact in some non-social action chains (Lorenz 1935).

The following facts illustrate another interesting point: the conditioning of different reactions in objectively the same or very similar situations often concerns different elements of such a situation.

As an example the brooding reactions of the Herring Gull may be compared with the reactions of feeding the young. The reactions of settling down on the eggs are evoked by a stimulus-situation including a few marks of the eggs, the nest basin, and a highly complicated combination of marks characterizing the place of the nest. Experiments show that the brooding response is entirely independent of the marks that characterize the bird's own clutch as different from other clutches. Even animals that lay "blue" eggs (in which the superficial brown pigment is lacking), that are so strikingly different from the normal brown eggs of the species that they are considered very valuable by "oölogists," do not prefer their own eggs to brown ones, though they might be expected to be conditioned to the conspicuous color of their eggs. The learning process is confined to those marks of the entire situation that characterize the *place* of the nest.

From the 5th day after hatching on, the reactions of feeding the young are confined to the bird's own young. The adults, conditioned to the individual characteristics of their own young, feed them irrespective of their location in the nest. The difference as compared with the brooding reaction is

obvious. Equally obvious is the fact that both kinds of response fit in both cases in the special structure of the environment: the eggs do not move away from the nest, whereas the chicks do. This is, of course, no solution of a problem, but merely the recognition of its presence.

The Means of Communication Proper

A comparative study of the means of communication ("language") in different species reveals an enormous diversity. All these different processes of communication can be classified in two groups. A flight reaction of one member of a flock of Jackdaws or Sandpipers or of a shoal of Sticklebacks will evoke flight reactions in the other members of the flock. When one member of the flock starts eating, the others join. Here the Actor induces the same movement in the Reactor.

Threatening behavior of a territorial male Stickleback induces flight reaction in a stranger Stickleback. The distress call of a young Duckling induces maternal activities in the mother. Aggressive behavior of the male Bitterling, which defends a mussel *(Anodonta)* causes the mature female to swim downward to the mussel, where she will deposit her eggs. In all of these cases the response of *R* is different from *A*'s action.

The question arises: which processes elicit *R's* activities? By which means do *A*'s activities influence *R*? The answer to this question differs in two respects from that expected at first glance. Some instances may illustrate this.

A male Stickleback ejaculates sperm shortly after a female has laid eggs in the nest he built. Some simple experiments show that the ejaculation is released by the smell of fresh, unfertilized eggs. Optical stimuli have no influence, although the eggs are plainly visible. Incapability of the optical apparatus cannot account for this because the eye is capable of good color, form and movement reception, which appears when an analysis of other reactions is made. This leads to the conclusion that the releasing behavior of *A* may act merely through part of *R*'s sense organs, although potential stimuli for the other sense organs may be "broadcasted" by *A*.

There is, however, a second restriction. The eyes of a fourteen day old Blackbird enable it to discriminate form fairly well. When directing its begging movements to the head of the adult, it reacts to recognition marks of less than 2 mm diameter.

The stimulus situation required for the *releasing* of the begging movements does not include any form character, as will be remembered. Every figure, provided it is larger than 3 mm in diameter and moving above the eye level evokes a full response, definitely independent of its shape.

Lorenz, in one of his studies on the sociology of the Jackdaw, emphasized a still more striking example of this phenomenon. A Jackdaw reacts to the sight of a predator which is carrying a Jackdaw by giving the alarm call. This again evokes an attack by all members of the breeding colony. The alarm call is released by a very vaguely determined stimulus situation, for a man

wearing a black bathing suit and even a Jackdaw carrying a black feather to its nest evoked the reaction. Simultaneously some other reactions e.g., sex behavior, are confined to an individual Jackdaw. The birds can distinguish at a glance between two individuals and by this capacity they show that their optical receptors do not cause them to react in the same way to a Jackdaw and a bathing suit.

Numerous instances of the same phenomenon could be given. They all lead to the conclusion that central processes are at work in deciding which factors of the receptual field have or have not releasing or directing effects on a certain reaction. One of the main points in Von Uexküll's "Umweltlehre" has been the demonstration of the fact that every reaction of an animal has its own "releasing mechanism" (Auslösendes Schema). The mechanism, or the coupling of special stimulus and special reaction, is innately fixed in many cases, even in the highest mammals, man included. Undoubtedly a human female has an inborn mechanism pertaining to feeding and other reactions toward the baby. The following characteristics of the latter probably belong to this mechanism: crying, performance of maladjusted movements, and the possession of thick cheeks. The courtship of a mature human male in presence of a female certainly responds to an innate mechanism of the female by a display of strength, smartness or by another form of superiority over other males. Of course in both cases the innate mechanism is modified and highly supplemented by important learning processes.

It does not seem to be generally recognized that different reactions, evoked by and directed toward the same object in different situations may have different mechanisms. For instance, an animal may have different reactions to a sex partner: copulation, joining it in feeding, calling it, assisting it in nest building, or relieving it in incubation. Each reaction may have a different releasing mechanism. Sometimes, when a partner is defective in some way in its reaction pattern, an animal may take two partners, one principally for coition, and the other for assistance in nest building. Consequently it is misleading to speak of the "mechanism" (Schema) of the "sex partner" or of "the social companion," since one can speak only of the mechanism of a certain reaction. Likewise, it is futile to try to corroborate or to negate a conclusion regarding the releasing mechanism of reaction (a) in species (S) by studying the mechanisms of the same (and much less of another) reaction in species (X). There are as many mechanisms as there are behavioral units.

The concept of "mechanism" involving few recognition marks raises one fundamental question: are these marks the only effective factors in an absolute sense or can an influence of the other parts of the sensory field, however slight, be demonstrated? In the latter case, the difference between effective and non-effective parts of the sensory field would be merely one of degree.

Although until recently experimental methods have been too gross to justify a definite conclusion, there are some available facts that elucidate the question.

The male *Gasterosteus aculeatus*, when ready to receive a female in its nest, shows the same first reaction to every approaching Stickleback, irrespective of its being a red male (—a male in full breeding dress), a pale male, an immature female or a mature female. Many other animals are welcomed in the same way. The response of the other individual determines either the male's attack or its guiding behavior. The same state of affairs is found in animals of various groups: spiders (Holzapfel), the Squid *Sepia officinalis* L. (L. Tinbergen 1939), the Fighting Fish *Betta splendens* Regan (Lissman 1932), pigeons (Craig 1909, Whitman 1919, Heinroth 1928) and other birds (Tinbergen 1935, 1939). We must conclude that the mechanism of this first reaction possesses only a few recognition marks.

However if a male and a female are presented to the male at the same time, he will show slightly different responses to them, which proves that the releasing mechanism must include some differentiating marks of either female or male. This has been observed in *Gasterosteus*. These differentiating marks are unimportant, for the reaction occurs in optimal or almost optimal intensity whether they are present in the external situation or not. It is not known, however, whether these additional marks belong to the inborn mechanism or are caused by individual conditioning.

Despite the emphasis on the "innate releasing mechanism" I am fully aware of the more complicated means of communication. As a matter of fact, the more highly organized mammals, especially man, probably have few, if any, unmodifiable mechanisms, and the mechanism of every reaction has been changed into an amazingly complicated nervous connection. Yet as emphasized before, the underlying mechanism can often be recognized.

On the basis of the previous discussion it should be stressed that there is no controversy between the assumptions of a conditioned response and an innate releasing mechanism. A response cannot be conditioned unless it is present before the conditioning. Conditioning means changing something that is already present, but it does not bring about a new reaction.

The Behavior of A

The activities of *A* which give rise to *R's* response, may result in the stimulation of different sense modalities. In the preceding paragraphs, several instances of this were given. Often an activity which has communicative value may stimulate *R* by means of more than one modality. Even if restricted to one modality, the stimulus is almost always a rather complicated one. A female Stickleback in egg laying mood prefers following red males which move in a special way. This special movement, together with a color pattern, form the optimal situation for the release of the female's reaction.

Often the behavior as well as the displayed structure which serve as a means of communication differ from the behavior or structure employed in any of the other activities of the animal; in short by specialization they are adapted to their communicative function.

The adult thrushes which evoke the gaping movements of their nestlings, accomplish this without any specialization. Since they are moving, larger than 3mm., and are in the upper hemisphere of the young's optical field, their communications do not evolve from activities other than actual feeding nor are they brought about by the use of special structures.

Other species of altricial birds display special activities which serve to evoke the gaping reactions of the nestlings. Kuhlmann (1909) says about the Redwing Blackbird that the young react to "the special clucks of the parent birds, used especially for this purpose. . . ." (p. 64).

Defecation of the nestlings ordinarily occurs shortly after feeding, and the adult bird waits for the feces to carry them off. In the Wren-Tit, Erickson (1938) observed that "If none is forthcoming, the adult often pecks the nestling in the region of the anus as if to stimulate defecation." (p. 292).

Although further analysis in both cases would be necessary to ensure that these activities are especially adapted to communication, the examples suggest a way in which specialized movements may arise.

Such movements are often augmented by conspicuous structures. When a Herring Gull feeds its day old young, it points its bill to the bottom, and, after regurgitation, takes a tiny piece of food between the mandibles and presents it to the young. The newly hatched chick has an innate tendency to peck at all red patches and as a result it gets food by pecking at the red patch on the parent's bill (Goethe 1937). This is the only known function of the red spot. It would be worth while to study the reactions of the chicks of those species that have no red spot, or of species with other color patterns on the bill (Ring Billed Gull).

A more specialized case is offered by the wing patterns of Anatidae. Every species has its own pattern so that a colored picture of duck's wings works "like a flag-directory" (Lorenz). In fact, they have about the same function as a flag viz., to designate the species. Heinroth has given a most convincing illustration of this principle: he observed in the Berlin Zoo, that Anatidae with black and white wing marks evoked social reactions only in those species possessing the same wingmarks regardless of taxonomic relationship.

Lorenz (1935) called all movements and structures producing a response in the social companion "Auslöser" ("releasers"). The more general term *signal* is perhaps preferable since the activities and structures may have releasive or directive influences, or both simultaneously. The smell of unfertilized eggs of the Stickleback, for instance, releases the fertilizing movements of the male, although it certainly does not direct them; orientation is optical and tactile, but not chemical. For the Lapwing, the danger call may have primarily releasive function, whereas the white tail mark may have primarily directive function. It is quite possible, therefore, that the concept of "signal" should be subdivided into "releaser" and "director," although most of the signals may have both functions.

Lorenz' concept of signal offers the best explanation of the function of conspicuous structures and modifies the views derived from Darwin's thesis of sexual selection. The basic assumption of the theory of sexual selection implies that the conspicuous structures serve to influence sexual or fighting responses in other individuals. A few examples will suffice to show that signals may serve for the release of many responses other than sexual or fighting ones. The red spot on the Herring Gull's bill and the wing marks of the Anatidae were mentioned above. Two other kinds of signals can be found in the nestlings of many Passerine birds. When "gaping," the inner surface of the mouth is shown; it is very conspicuously colored, often displaying various patterns in different species. Often this pattern is highly specialized, as for instance in the European Bullfinch. For excellent pictures of these "Sperrachen" the reader is referred to Heinroth's "Die Vögel Mitteleuropas." The other signal structure found in Passerine nestlings is an erectile ring of conspicuously colored feathers around the anal aperture. This signal is displayed shortly before defecation and releases as well as directs the feces taking movements of the adult.

A very striking demonstration of Lorenz' thesis that special signals of *A* are connected with special reactions of *R* is described by him of the Mallard. The adult's relieving reactions to a chick in distress are released by the chick's distress call. This call is quite similar in different species. If a chick of another species is caught by the experimenter, its distress calls will cause a mother Mallard to attack the predator and force him to drop the chick. As soon as the chick is saved, the Mallard will attack and kill it. According to Lorenz, the guiding and brooding activities of the adult female are dependent, not on the distress call, but on the color pattern of the young's head and back, which is much more specific than are the calls.

Lorenz pointed out that signals have two general properties: they are 1) relatively simple, and 2) specific ("unwahrscheinlich"), that is to say, they are different from other structures that may occur in *R's* environment. The simplicity seems somehow to be connected with the fact that every inborn mechanism is a relatively simple complex, composed merely of a few marks. This empirical statement, of course, has no explanatory value and only points out a problem.

The specificity of a signal is like that of a key. It is obvious enough in the morphological signals. It should be emphasized that the same holds true for the signal *movements*. The movements of a female Stickleback ready to lay eggs serve as a signal for the courting male. Her behavior consists of swimming toward the male, holding her body in a semivertical position, pointing the head upward as shown in Fig. 2. This is indeed an unique movement among fishes. Experiments have shown that dead females, dead males (provided they were not red) and even dead fishes of other species, when held in this posture, were capable of releasing the male's guiding behavior.

Sounds that have communicative value are often very specific too. The

specificity of the song birds and of the migration calls of birds are convincing proof of this.

Since few cases of the functions of a signal structure or movement have been studied seriously the reported observations indicate the desirability of further study of different kinds of signals. The results of the available studies justify the assumption, as a working hypothesis, that conspicuous and highly specialized structures, whose participation in non-social processes cannot be found have a social, communicative function.

A comparative study of signals in closely related species should reveal suggestions of their phylogenetic origin. Although such a comparative study of special groups has yet to be carried out despite a start in some groups, one general rule is readily tenable: Signal movements may occur without morphological structures, but not vice versa. Heinroth emphasized the fact long ago that whenever a conspicuous structure is found in a bird, the bird possesses one or more innate reaction patterns which utilize these structures. On the other hand if two species perform similar movements, they are "augmented" by a special structure in one of them, whereas this is not so in the other. Lorenz gives several examples from Ducks (1935) and Grebes (1938). The obvious conclusion is: "the ceremony is older than its organ." Actually more arguments seem to suggest the conclusion that special inborn behavior elements are probably more constant in evolution than many morphological structures. For instance, no single morphological character has been found in all members of the family of the Columbidae (pigeons) yet they all have a behavioral trait not known in any other bird viz., they "pump" while drinking. Of course, this constancy during evolution effects merely one category of behavioral elements and not the more adaptive elements.

In much the same way as the evolution of morphological structures is studied by comparative morphology, the evolutionary origin of the movements with signal function can be revealed by comparative behavioral study.

Since the conclusions and arguments presented in the following are not based on previously published material, they must be afforded a more detailed treatment.

A bird, starting to fly, presses its feathers against the body and thus appears as thin as possible. At the same time its neck is more or less stretched as the bird stands in an alert posture. In the Herring Gull and in other species, this behavior has communicative value causing the companions to react to it promptly. The "intention" to start walking or flying is expressed in an even more pronounced form in other birds e.g., in the Anatidae, in which special movements of the head, often recognizable as incipient or preparatory flight movements, precede the take-off. Heinroth (1910) calls these kinds of motions "Intentionshandlungen"; I propose calling them "*preparatory movements.*" They presumably play a part in many inter-individual relations. Often the preparatory aggressive movements have a threatening function, especially so in *Gasterosteus aculeatus* L. By special planting of the vegetation it is possible to have two males of this species occupy a territory and build a nest in one relatively small tank. Repeated

fights result in a sharply defined border of the two territories. After some time "border incidents" are reduced to alternating incipient attacks by both males, each of which in turn swims toward the other, causing the latter's retreat before any fighting begins. A series of back and forth movements follows. Exactly the same phenomenon was observed during boundary disputes between two male Snow Buntings (Tinbergen 1939). Pickwell (1931) describes a similar occurrence in the Prairie Horned Lark.

In many Anatidae, the preparatory flight movements were specialized during evolution and consequently they may scarcely be recognized as such.

Another category of incomplete movements are the "symbolic activities" as described by Portielje (1928, 1938). They are prevalent during the mating period: birds furnish many examples. Frequently birds show incomplete nest building movements before actual nest building begins. A female Yellow Bunting may take a piece of grass or moss in its bill, carry it for a few seconds and then drop it (Howard 1929). A common Tern may make some nest hollowing movements shaping a very incomplete "scrape" and then abandoning it (Tinbergen 1931). Howard (1929) called attention to the incomplete coitions which occur in many species of birds, especially at the beginning of the breeding season. It is characteristic of all these movements, that if the external stimulating situation should be optimal the incompleteness of the actions must then be attributed to a lack of internal stimulation.

Since the knowledge of both preparatory and symbolic movements is still very fragmentary, further analyses of these certainly are needed.

The symbolic activities appear to have evolved as "language" from many sources. Many signal actions are exactly alike or very similar to symbolic actions. A striking case is found in the courtship of the Common Tern. This species, like other Terns, uses a fish in courtship. The courtship develops in three phases, each lasting several days. The first phase is performed in flight, a fish-bearing partner being joined by a fishless partner with both participating in a ceremonial flight. During a later phase of the courtship the members of such a pair (still temporary) alight on the ground and assume a special walk with the fish bearing bird still keeping its prey. During a third phase the fish is fed to the partner and often copulation results. This sequence of events leads to the interpretation of the first phases as "symbolic feeding." This symbolic feeding is always a part of the premating behavior of the species.

Symbolic feeding shows two characteristics that differentiate it from the real feeding which occurs during the incubation period, when the non-incubating partner feeds the incubating bird, and from the subsequent feeding of the young. First, the movements are markedly different from the real feeding movements. The fish bearer bends its head and makes a sound typical for this situation whereas the other bird does not make the begging movements but assumes another attitude, equally different from the begging movements.

Second, the courtship is often performed in exactly the same way, *but without the fish*. This elimination of the adequate object and the "formalization" of the movements are probably principles of very wide application. A comparative review of the courtship activities of widely different representatives

of the Terns, with especial reference to these "fish-flights" would be of great interest. As in comparative morphology, this work should be based on arranging series of behavior elements as found in related species, but at present the descriptions of these functional units which are to represent the members of such series are almost entirely lacking.

A third category of formalized signal movements has a different origin. During boundary flights, during the presence of a predator near the nest or young, and during courtship birds often display activities which closely resemble movements belonging to another functional cycle. In the Snow Bunting, for instance, threatening males often show movements highly simulating feeding movements, but which on careful observation appear to be incomplete; food is never taken and the bill does not even reach the ground (Tinbergen 1939). This behavior is shown especially during boundaray disputes, when neither of the two birds actually attacks, but both indulge in threatening. I propose calling these incomplete feeding movements *"substitute feeding,"* because they replace fighting activities induced by the situation.

Substitute feeding has been observed in several species of birds. I saw it performed by domestic cocks, which made pecking movements during short pauses in a prolonged fight. Lorenz (1935) observed the same. Pickwell (1931) also observed it in the Prairie Horned Lark during boundary fights, and I saw it under the same circumstances in Skylarks, Blue Tits and Coal Tits (Tinbergen 1938). Makkink (1936) describes substitute feeding in the European Avocet; food "mowing" is shown by this species when human beings come too near the nest; it is likewise shown during hostile encounters of Avocets *inter se*. The following observation, made by J. J. Ter Pelkwijk, refers to substitute feeding in the Garganey. A female with chicks foraging along the borders of a small canal, left this border as soon as the observer came too near, and as long as he stayed, the bird swam restlessly to and fro in the open water in the centre, stretching its neck and every now and then making the typical feeding movements ("slobbering") of this species. As soon as the observer withdrew, she resumed her ordinary attitude and continued foraging at the border. Since the water in the centre was quite clear, open and not covered with food plants as at the border, the observed movements probably should be interpreted as substitute feeding.

In species like the Avocet and the Garganey, which have very specialized feeding movements, the interpretation of substitute activities as feeding is easy; in species with less specialized movements the pecking movements might be, e.g., incomplete nesting movements.

Carpenter (1934) reports behavior which possibly is related to substitute activities in the Howling Monkey: "A most interesting type of behavior has been observed in two situations: (1) The observer is quiet and partially concealed; a howler behaves as if seeking to get a better perspective by approaching nearer to the observer; it may casually pluck leaves and eat them as it approaches, (2) an animal may approach another and begin feeding, continuing to eat casually until within striking distance of the animal approached; then it may spring on the second individual and begin playing. I have observed similar sham feeding as the clan males approached a solitary male" (p. 37). Carpenter's interpretation of this case differs considerably from the interpretation of substitute activities in lower Vertebrates which will be presented in the following.

Another common substitute activity in birds is preening. Huxley (1914) describes preening activities as part of the courtship in the Great Crested Grebe, and calls them "habit preening." A very clear cut example was observed by me in the European Starling. A male Starling, observed singing in front of a hole in March, showed aggressive behavior to all other Starlings which came too close to the hole. Whenever another Starling alighted within a few meters' distance he walked in a lowly bent, flat attitude towards him. When the stranger flew away, he reoccupied his singing post

and resumed singing; but in case the other stayed, the owner did not actually attack, but remained in front of him and instantly began to preen his feathers, with "exaggerated" vigor. As soon as the other went on, he instantly stopped preening and returned to his singing post. This was observed repeatedly. According to Lorenz (1935) the Crane *Megalornis g. grus* (L.) shows preening under the wing in hostile situations. In courtship, substitute preening is used in a more or less formalized way by several Anatidae e.g., the Shell-Drake (Makkink 1931) and the Grey Lag Goose (Heinroth 1910, Lorenz 1935).

Other substitute activities observed in birds are: sleeping, and probably singing. Instances of these types, however, seem to be less common than feeding and preening.

The different situations in which substitute activities occur allow a psychological interpretation. In all cases in which substitute activities are observed, external and internal causes seem to be sufficient to evoke the normal reaction in maximum intensity, but the normal reaction seems to be blocked in some way. Blocking of the normal reaction appears to be the result of different conditions.

First, the animal may be under the influence of two antagonistic drives, the simultaneous expression of which is a physical impossibility. In the boundary disputes, as well as in the situation "human being too close to the young," flight and attack are evoked at the same time. The result is that expression in both functional cycles is inhibited and that a substitute action occurs.

In the case of substitute activities appearing during courtship, the normal sexual responses seem to be blocked in another way. Substitute feeding as part of the courtship of the male Snow Bunting occurs only when the female refuses copulation initiated by the male. Since coöperation of the female is necessary for coition, the normal reaction of the male is blocked by the lack of the external releasing situation and the reaction chain breaks off. At this moment the substitute activity appears. It seems to me that this is the main cause of the appearance of substitute activities in courtship. The situation of the antagonistic drives, however, may also play a part. In the European Blue Heron the male's sexual drive is obviously counteracted by the flight drive and a newly mated individual repeatedly defends itself against too close an approach of the partner (Verwey 1930). A similar antagonism between flight reaction and sexual attraction might play a role in other birds too.

Still another situation may cause substitute activities. Exhaustion of the normal reaction after a number of performances may result in substitute behavior. A Whitethroat shows "injury feigning" when disturbed at the nest. It will repeat the reaction twice, thrice, and then sit down somewhere and preen. Preening in this case might be interpreted as substitute preening.

Huxley (1914) in describing substitute preening in the Great Crested Grebe calls it "habit preening." The fact, however, that the substitute actions appear to be fixed and characteristic of the whole species, suggests that they consist of inborn patterns. This seems to apply equally well to several of the substitute activities of the highest mammals. Man certainly has the innate tendency of substitute preening (scratching himself behind

the ear) in certain situations. Dr. G. Finch draws my attention to the fact that Chimpanzees when they are not allowed to take expected food, show typical substitute actions, which are approximately the same for every individual. Scratching is almost always involved.

Certainly in Man and presumably in lower animals too, habit may influence the kind of substitute action. Winding one's watch and lighting a cigarette may be mentioned in this connection.

MacDougall's thesis ".... the animal in which any instinctive impulse is excited does not suspend action, even though the object be remote; the impulse probably always expresses itself in action" (1931, p. 207) requires completion, for the animal does not display random movements, but shows very special behavior, viz., special innate or learned patterns. A closer study will be necessary to understand why special substitute activities are linked to special situations. A few suggestions may be given.

Herring Gulls show "substitute nestbuilding" when threatening birds which intrude into their territory (Tinbergen 1936, Goethe 1937). The same substitute nest building is displayed on the feeding ground when defending prey against a competitor. Though fights for food occur throughout the year, substitute nest building is limited to the reproductive season. This shows that the direction of the outlet varies with the endocrine condition of the animal.

During an investigation of the egg rolling movements of the Grey-lag Gooses Lorenz and I found that, if the internal, specific cause of the rolling movements was exhausted by repeated performance of the reaction, the external (sensory) stimulus offered by the situation "egg out of the nest" caused the animal to move straws to the nest instead of the egg. This suggests that the substitute action tends to "use" a pattern closely related to the normal reaction.

In the same way as described for the symbolic actions, these substitute activities have been subject to "formalization" and to loss of the adequate object during phylogeny. In the premating period the male Blue Heron often makes the "snap-movement," which was interpreted by Verwey as the fish-capturing movement without a fish. The same applies to all the feeding actions mentioned previously: the prey is invariably lacking. The preening movements made by the Shelldrake prior to coition is formalized to a great degree.

The process of formalizing, when accompanied by the loss of the object, often renders it extremely difficult to recognize the origin of a substitute activity. A territorial male Stickleback threatens its opponent by assuming a nearly vertical position, head down, and at the same time making biting movements. At present it is not known whether this is derived from the nest digging movements or from feeding movements. The digging is the first phase of nest building. It is hoped that a comparison with closely related species together with a careful observation of the variability of the threatening movement will bring the solution. It may be of significance that *Gasterosteus*

pungitus, a species which builds a hanging nest above the ground and which does not dig, has similar, though still more formalized made of threatening. This would point to its interpretation as a feeding movement.

Obviously not all substitute activities have necessarily communicative function. The point in question is that "signal" movements often have originated as substitute activities.

It is evident that this review of substitute actions is highly fragmentary and tentative. Further study of them as well as of the other signal movements is needed.

Causal analysis in sociology as well as in other sciences requires experimentation. A beginning has already been made and we owe much to the use of "Attrappen" (models, artificial animals, decoys) for the analysis of mechanisms. However, sociological experiments seem to call for special caution. Several published experiments show certain shortcomings which are apt to lead to (and have led to) premature conclusions, and therefore will cause needless confusion.

In the first place, no experiments should be started before simple observation of behavior in natural surroundings has discovered the outlines of the behavior patterns. This is important in two respects. First, the undisturbed course of activities always gives provisional clues to causes; owing to changing conditions "natural experiments" result, a fact emphasized by Selous long ago (1901), and stressed again by Verwey (1930) and by Lorenz (1935). Second, by watching undisturbed behavior without premature restriction to one functional cycle or even one reaction, one is forced to keep in mind that different reactions have different releasing mechanisms. The neglect of this fact has often caused needless scientific quarrels. As an example the discussions between Hess and Von Frisch (Von Frisch 1914) on the color discrimination of the honeybee may be mentioned here. Hess claimed color blindness, basing his view on good experiments, while Von Frisch, with equally convincing experiments, could prove color discrimination. The diversity of views was due to the fact that Hess analyzed the flight reactions, which are directed to the part of the visual field that offers light of the highest (subjective) intensity, while Von Frisch analyzed the feeding reactions which are directed to flowers of special colors.

The same confusion can still be found in studies of animal sociology. Allen found (1934) that a male Ruffed Grouse in sexual condition showed the same first reaction to approaching males as to approaching females of the same species. The author concludes that the male Ruffed Grouse (and "birds" in general) does not discriminate between the sexes. Yet the next reaction in the chain is different towards females than towards males. This second reaction, therefore, shows that the bird can discriminate. In the same way one could conclude that a Jackdaw cannot discriminate between a bathing suit and a Jackdaw because it shows the social alarm call to both. In this species other reactions also show that the animals discriminate much more sharply than could be expected by examination of the alarm call.

Another source of confusion affects directly the nature of an experiment

in general. The sensorial perception which releases *R's* reaction is always an interrelated whole of several factors, a "Gestalt". If the experimenter presents the optimal situation, less one factor, the reaction will often occur "just as well" as after optimal stimulation. A slight difference of intensity may escape attention owing to the fluctuations due to other causes. This result, however, does not permit a conclusion regarding the value of the isolated factor. The same factor can be shown to exert influence when added to a situation which by itself would not evoke the reaction. The following facts may serve as an illustration. The Three-spined Stickleback is sexually dimorphic. In order to test the question whether the red belly of the male had any influence on the female's egg laying activities, Leiner (1930) observed courtship and egg laying in monochromatic light of different colors. Finding the behavior following a "normal" course, he concluded that the colors of the male were without influence. Ter Pelkwijk & Tinbergen, however, could show that the red color was effective by evoking the female's reactions by means of red painted dead females, which were ineffective before painting. The species is capable of discriminating red, as shown by experiments concerning the feeding reactions.

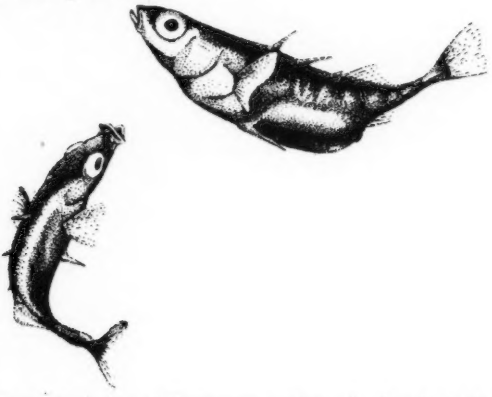


Fig. 2. Courtship-display of *Gasterosteus aculeatus* L. Female (right) in "signal"-attitude, indicating readiness to follow the male (from Ter Pelkwijk & Tinbergen 1937).

The difference in methods is a minor one, though of considerable importance. The dead female lacked sufficient marks to evoke the reaction. When the factor *red* was added, the releasing value of the situation was increased. Living animals apparently offer signal movements which remain effective after the color factor has been eliminated.

The complex of influential factors in the Gestalt can be effected by the intensity of the animal's motivation. Abnormally high motivation has a profound influence on the structure of the perceptual field. Factors that are influential in a normally motivated animal may become entirely worthless

when the animal's motivation rises. In reflex-like, released movements, this results in a "lowering of the threshold" of the reaction. In oriented directed movements, the disappearance of parts of the perceptual field is shown by the fact that the animal ceases to direct its activities towards certain details (Tinbergen & Kruyt 1937). During experiments it is necessary, therefore, to keep motivation as "normal" as possible, or at least at a same degree throughout. The fact that an isolated male canary courted a woolen doll representing a chick does not allow the conclusion that a normally motivated male would not require some more recognition marks in its sex partner (Koehler 1926).

Another point of importance is the fact that one signal may have more than one function. It has been proven by experiment that the red color of the male *Gasterosteus* has a signalling function to other males, evoking attack in a territorial male, and evoking flight in a male outside of its territory. Other experiments already cited prove that the red color also has an influence on the female. The red belly, therefore, is at the same time a "gladiatorial vestment" and an "attracting device".

Consequently, from experiments showing the influence on the male only, it cannot be concluded that a certain structure has no influence on the female. To mention a concrete example: the fact that the "moustache" of the male Flicker releases attack of a territorial male, allows by no means the conclusion that this is its only or even its primary function. Yet Noble went beyond this conclusion by stating: "It follows that sexual selection in the Darwinian sense, that of female choice, has played no role in enhancing the color of the Flicker." (1936, p. 281).

I am aware of the fact that this review of social organization is very schematic. I would like to stress once more that in most cases communication processes are much more complicated than mere fixed innate reactions. Recognition of the existence of signals does not imply the assumption that every signal works by means of an immediate, innate reaction of *R*. Many "internal" processes in *R* may influence the mode of response: endocrine processes and the nervous processes of summation, learning and all so-called "higher mental processes."

A special kind of these internal nervous processes may be mentioned because it concerns an important problem of evolution: the problem of sexual selection. Apart from having a momentary or a summative stimulating influence, signal structures may enable *R* to *make a choice* between different individuals which show differences of degree in the development of structural or behavioral signals. That in species with a pronounced sexual dimorphism the animals of one sex (ordinarily females) make a choice between several individuals of the other sex, is probable in the case of some birds. Actually this has been proven by Noble (1938) in the case of the Jewel Fish. He was able to evoke an expansion of the male's erythrocytes by injection with yohimbine without changing its behavior. The females preferred the excessively colored males.

SUMMARY

Social integration depends on relations between Actor and Reactor.

Such a relation comprises always an action of *A* influencing *R's* sense-organs; subsequently through nervous system and effectors *R's* response is effected.

Activities of R. To find the external causes, *R's* behavior has to be divided into its components. Special mention is made of two groups of behavioral elements, differing according to the way in which sensory stimuli influence them: reflexes and similar reactions which are merely *released,* and oriented movements (tropisms, taxis) which are *directed* by external stimuli.

Arguments are presented for the conclusion that even "simple reactions" of *R* may be composed of two simultaneously working mechanisms, an "instinctive action" (Lorenz) and a "taxis".

Endocrine and neural processes (summation, conditioning, "higher mental processes") may influence the innate mechanism (Schema).

Learning processes may be confined to special reactions and to special parts of the perceptual field.

Means of communication proper. A's behavior may evoke either the same behavior in *R* or a different reaction.

In two respects the external stimuli influencing *R's* reaction may be only part of the external situation received by *R's* sense organs: a) only one or two of the sense organs may have influence, b) only some factors of the receptual field may be effective. Thus we are led to the conclusion that there must exist special S-R sequences (mechanisms, Schemata) between certain factors of the sensorial field and certain reactions.

These innate mechanisms are also the basis of the highly modified, conditioned and other "higher" responses of *R.*

The behavior of A. A's activities provide signals for *R.* Movements that act as signals are sometimes "emphasized" by morphological structures.

Signal movements, like morphological signals, are often very specific ("unwahrscheinlich").

Signal movements have evolved from "preparatory movements," "symbolic actions" or "substitute actions".

Substitute activities appear when the reaction evoked by external and internal stimuli is blocked, either by an antagonistic reaction, or by lack of stimulation for the next reaction of the chain, or by exhaustion of the normal reaction.

Substitute activities, like symbolic actions, as signals have undergone profound changes during evolution: they became formalized and the adequate object was eliminated.

REFERENCES

ALLEE, W. C. 1931—Animal Aggregations. Chicago.

———1938—The Social Life of Animals. New York.

ALLEN, A. A. 1934—Sex rhythm in the ruffed grouse (*Bonasa umbellus* L.) and other birds. Auk **51**:180-199.

ALVERDES, F. 1925—Tiersoziologie. Leipzig.

CARPENTER, C. R. 1934—A Field Study of the Behavior and Social Relations of Howling Monkeys *(Allouetta palliata)*. Comp. Psychol. Monographs **10**:1-168.

CRAIG, W. 1908—The voices of pigeons regarded as a means of social control. Amer. Journ. Sociol. **14**:86-100.

———1909—The expression of emotion in the pigeons. I. The Blond Ring-dove *(Turtur risorius)*. Journ. Comp. Neur. Psychol. **19**:29-80.

DARLING, F. FR. 1938—Bird Flocks and the Breeding Cycle. Cambridge.

DEEGENER, C. 1918—Die Formen der Vergesellschaftung im Tierreich. Leipzig.

DIRCKSEN, R. 1932—Die Biologie des Austernfischers usw. Journ. f. Ornithol. **80**:439-558.

ERICKSON, M. M. 1938—Territory, annual cycle, and numbers in a population of Wren-tits *(Chamaera fasciata)*. Univ. Calif. Publ. Zool. **42**:247-334.

FRISCH, K. VON. 1914—Der Farbensinn und Formensinn der Biene. Zool. Jahrb. Allg. Zool. Physiol. **35**:1-188.

GOETHE, F. 1937—Beobachtungen und Untersuchungen zur Biologie der Silbermöwe (*Larus a. argentatus* Pontopp.) auf der Vogelinsel Memmertsand. Journ. f. Ornithol. **85**:1-119.

HEINROTH, O. 1910—Beiträge zur Biologie, insbesondre Ethologie und Psychologie der Anatiden. Verh. V. Internat. Ornithol. Kongr. Berlin: 589-702.

HOWARD, H. E. 1907-1915—The British Warblers. 9 Parts. London.

———1929—An Introduction to the Study of Bird Behavior. Cambridge.

HUXLEY, J. S. 1914—The courtship habits of the great crested grebe *(Podiceps cristatus)*; with an addition to the theory of sexual selection. Proc. Zool. Soc. London :491-562.

———1923—Courtship activities in the red throated diver (*Colymbus stellatus* Pontopp.); together with a discussion of the evolution of courtship in birds. Journ. Linn. Soc. **35**:253-291.

KOEHLER, O. 1926—Uebersichtsreferate der Sinnesphysiologie. Jahresber. ges. Phys. **1926**:823-936.

KUEHN, A. 1919—Die Orientierung der Tiere im Raum. Jena.

KUHLMANN, F. 1909—Some preliminary observations on the development of instincts and habits in young birds. Psychol. Rev. Monogr. **11**:49-85.

LEINER, M. 1930—Fortsetzung der oekologischen Studien an *Gasterosteus aculeatus*. Zeitschr. Morph. Oekol. Tiere **16**:499-541.

LISSMANN, H. W. 1932—Die Umwelt des Kampffisches (*Betta splendens* Regan). Zeitschr. vergl. Physiol. **18**:65-112.

LORENZ, K. 1931—Beiträge zur Ethologie sozialer Corviden. Journ. f. Ornithol **79**:67-120.

———1935—Der Kumpan in der Umwelt des Vogels. Journ. f. Ornithol. **83**:137-214; 289-413.

———1937—Ueber die Bildung des Instinktbegriffes. Naturwissenschaften **25**:289-300; 307-318; 324-331.

———1938—Ueber das Mitteilungsvermögen der Tiere. The Hague.

——— AND N. TINBERGEN. 1938—Taxis und Instinkthandlung in der Eirollreaktion der Graugans. I. Zeitschr. f. Tierpsychol. **2**:1-29.

MACDOUGALL, W. 1931—An Outline of Psychology. 5th ed. London.

MAKKINK, G. F. 1931—Die Kopulation der Brandente [*Tadorna tadorna* (L.)]. Ardea **20**:18-21.

———1936—An attempt at an ethogram of the European avocet (*Recurvirostra avosetta* L.); with ethological and psychological remarks. Ardea **25**:1-62.

MURCHISON, C. 1935—A Handbook of Social Psychology. Worcester.
NOBLE, G. K. 1936—Courtship and sexual selection of the flicker *(Colaptes auratus luteus)*. Auk **53**:269-282.
———1938—Sexual selection among fishes. Biol. Reviews **13**:133-158.
———AND W. VOGT. 1935—An experimental study of sex recognition in birds. Auk **52**:278-286.
TER PELKWIJK, J. J. AND N. TINBERGEN. 1937—Eine reizbiologische Analyse einiger Verhaltensweisen von *Gasterosteus aculeatus* L. Zeitschr. f. Tierpsychol. **1**:193-200.
PICKWELL, G. B. 1931—The prairie horned lark. Trans. Acad. Sci. St. Louis **27**:1-153.
PORTIELJE, A. F. J. 1928—Zur Ethologie bezw. Psychologie der Silbermöwe, *Larus a. argentatus* Pontopp. Ardea **17**:112-149.
———1938—Dieren Zien en Leren Kennen. Amstersdam.
SCHJELDERUP-EBBE, TH. 1922—Beiträge zur Sozialpsychologie des Haushuhns. Zeitschr. f. Psychol. **88**:226-252.
SELOUS, E. 1901—Bird Watching. London.
TINBERGEN, L. 1939—Zur Fortpflanzungsethologie von *Sepia officinalis* L. Arch. Néerl. Zool. **3**(2/3):323-364.
TINBERGEN, N. 1931—Zur Paarungsbiologie der Flusseeschwalbe *(Sterna h. hirundo* L.). Ardea **20**:1-17.
———1935—Field observations of East Greenland birds I. The behavior of the red necked phalarope (*Phalaropus lobatus* L.) in spring. Ardea **24**:1-42.
———1937—Ueber das Verhalten kämpfender Kohlmeisen (*Parus m. major* L.). Ardea **26**:214-215.
———1939—Field observations of East Greenland birds. II. The behavior of the snow bunting [*Plectrophonax nivalis subnivalis* (Br.)] in spring. Trans. Linn. Soc. New York (in press).
——— AND W. KRUYT. 1937—Ueber die Orientierung von *Philanthus triangulum* Fabr. III. Die Bevorzugung bestimmter Wegmarken. Zeitschr. vergl. Physiol. **25**:292-334.
VERWEY, J. 1930—Die Paarungsbiologie des Fischreihers. Zool. Jahrb. Allg. Zool. Physiol. **48**:1-120.
WATSON, J. B. AND K. S. LASHLEY. 1915—Homing and related activities of birds. Papers Tortugas Lab. Carnegie Inst. Washington **7**:1-84.
WHITMAN, CH. O. 1919—The Behavior of Pigeons. Washington.

ZOOLOGICAL LABORATORY OF THE UNIVERSITY,
LEIDEN, THE NETHERLANDS.

DISCUSSION

MacGinitie: Can learning be a part of the experience of birds if that learning has to do with something not having been repeatedly a part of the evolutionary experience? In the evolutionary experience of a certain bird species there are many situations which reoccur many times. Can a bird learn in any case without a background in this evolutionary experience?

Tinbergen: There is no evidence for this influence of "evolutionary experience". The only experiments I know of are those of MacDougall with rats which showed that learning ability for a certain situation was improved in the offspring of trained generations even after application of a contra selection. However, this work has been criticized rather severely by geneticists.

MacGinitie: I have seen birds and mammals in circumstances in which they could not learn much of benefit to them. For instance, I have seen a woodpecker drill a hole for acorns in the side of a house where it was thin, pack into it perhaps a bushel or two of acorns and starve during the winter because he couldn't get at the acorns. In cuts made during road building gophers with a tendency to close an opening expend a

great deal of useless energy by working themselves poor trying to close that hole opening on a vertical surface of a road cut. These experiences do not occur every day.

Tinbergen: Apparently, the woodpecker offers an example of an immediate reaction to a few elements of the external stimulating situation, and that it did not occur to him at all that the wall of the house was *not* solid. Before interpreting such observations it should always be considered that an animal often, or perhaps always, does not see the environment as we see it. It seems quite possible to me that the storing reactions follow "automatically" the drilling of the hole, and that the difference between solid and non-solid wall did not exist at all for the bird. Consequently, the storing activity would not be a failure but a satisfaction, and there would be no incentive for a change of behavior by learning.

Emerson: Early naturalists were inclined to assume function in everything they saw. Some of the criticism applied to the naturalist and also to modern ecology is due to such superficial guessing. At the same time modern experimentation of this type is showing that many of these organisms do have functional relationship to the environment. The mechanism of natural selection could explain these functions reasonably well. Nevertheless, naturalists dealing with a great many species of the same genus are impressed by the number of seemingly non-functional characteristics. It is unnecessary to assume direct function for every specific characteristic according to modern genetics. If a character develops through selection, the genes involved may influence other structures in the body.

Tinbergen: Obviously, a function can not be found for every structure. A few hairs or spines on the thorax of an insect may be mere by-products and, in a sense, be without function, but in all cases of highly specialized structures it is necessary to assume a long, directed development, including many evolutionary steps, and in such cases it seems improbable that the structure should have no function.

Emerson: At the same time the existence of a highly specialized functional structure would be difficult to explain through any other process than by natural selection working on genetic variation through a long period of time.

Noble: Fighting in fish is correlated primarily with the territorial habit. It is well known that the female salmon seeks a breeding territory and that the males contend with one another for the opportunity of fertilizing the eggs. The literature contains various references to salmon having fought vicious battles, using their enlarged snouts as battering rams. In striking contrast to salmon, non-territorial fish, such as tuna, may migrate enormous distances without having any marked sexual dimorphism. The dimorphism of the salmon is definitely correlated with the territorial habit and not merely with long migration.

Emerson: The European cuckoo supposedly lays its eggs in various other birds' nests and the color markings of its eggs are the same as those of the host. What is the explanation of this?

Tinbergen: It is well known that an individual cuckoo lays in the nests of the same species during its whole life, and that its eggs resemble those of the particular host very closely, and further that a cuckoo lays in the nests of the species that reared it. The fact that the cuckoo lays eggs of the same color as those of the host may be due, in part, to the selective influence of the host. Rensch showed that several host species removed eggs from their nests that differed too much from their own eggs. They threw out the egg differing from the majority of eggs, without recognizing their own eggs. When Rensch changed all eggs but one for an equal number of stained eggs, the birds threw out their own egg and incubated the stained ones.

Mayr: It is highly probable that the cuckoo will lay in the nest of the species by which she was raised but there is no proof for it. In Finland, several species of birds lay solid blue eggs. The cuckoos parasitizing on these species also lay blue eggs. In Germany, very few cuckoos lay blue eggs. On the other hand in the cow-bird, also a nest parasite, no such adaptation of the eggs has been observed. If a cuckoo does not find enough nests of her favorite host species, she will lay an egg into the nest of another species, whoch, however, may throw out that egg.

Analytical Population Studies in Relation to General Ecology

Thomas Park[1]

I

I should not think it necessary before this audience to dwell at length upon the biological reality of the population. Just as the morphologist and physiologist concern themselves with the cell and organism as structural and functional units, so, it seems to me, the ecologist centers his attention around the population. There is nothing esoteric or paradoxical in this viewpoint. Certain resemblances between cell, organism and population emphasize the common properties of these three entities, while, at the same time, the possession by the population of other characteristics stresses its biological uniqueness. It is these characteristics that give the population its individuality and make it so important from the point of view of the modern biologist; sufficiently so, apart from other possible considerations, to justify the existence of ecology.

A brief examination of some of the attributes of populations might be in order as a background for the discussion to follow. Among its common biological properties the population (1) possesses a definite structure and composition, constant for any moment of time but fluctuating with age; (2) is ontogenetic, exhibiting growth, differentiation and division of labor, maintenance and death; (3) is genetic, inheriting from each preceding generation a system of gene frequencies; (4) is integrated and coördinated, and (5) meets, as a unit, the full impact of the environment which may modify it and which, in turn, it may modify.

The distinctive features of the population are correlated with the fact that it is a statistical entity. This is not to admit that these features are hazy or impossible of definition. It is only a statement of the fact that the population is a group and, as such, exhibits group attributes and therefore must be measured and appraised in quantitative terms. There is nothing new in this statement. Since the essay of Malthus, sociologists, demographers and population students generally have been aware of this feature and have stressed it in their writings. One of the best formal statements about the general nature of the population has been advanced recently by Raymond Pearl (1937, pp. 52-53) who says:

[1] I take pleasure in acknowledging my indebtedness to the following investigators who criticized this paper in manuscript and offered constructive suggestions: Doctors W. C. Allee, William Burrows, G. P. DuShane, A. E. Emerson, C. R. Moore, Raymond Pearl, H. H. Strandskov and Sewall Wright.

A population is a group of living individuals set in a frame that is limited in respect of both time and space. The biology of populations is consequently a division or department of group biology in general. The essential and differentiating feature of group biology is that it considers groups as wholes. It aims to describe the attributes and behavior of a group as such, that is as an entity in itself, and not as the simple sum of the separate attributes and behavior of the single individual organisms that together make up the group. The concept of group attributes, separate and different from the attributes of the component individuals, is a familiar one in other fields. For example, the familiar measures of variation such as the standard deviation and the coefficient of variation, are quantitative expressions of a group attribute, namely, the shape of the distribution of frequency of the component individuals in respect of the character measured. Similarly, birth rates and death rates are quantitative expressions of group attributes, meaningless relative to any individual.

At the risk of seeming pontifical, I think it healthy to occasionally remind biologists, first, that it is the natural heritage of organisms to live side by side in a frequently intimate nexus that is both competitive and coöperative, and, second, that first-rate observational and experimental examinations of this nexus are important and to date woefully few in number. I am taking the position in this Symposium on Plant and Animal Communities that analytical population studies have something to offer to general biology and especially to ecological theory. I plan to develop this argument by asking a series of questions which will be answered, discussed or emphasized as the case may be. The proposed questions are as follows:

1. What are the focal points and what are the methods used in attacking population problems?
2. What are some of the significant experimental population studies?
3. What generalizations and concepts have arisen from these analytical studies?
4. How are these studies related to modern ecology and where have they succeeded and failed in contributing to ecologic theory?
5. What are some desiderata for population investigations?

There is one matter by way of definition that should be cleared up before proceeding. It will be noted in the paper that the term "population" is used, first, to represent an assemblage of individuals belonging to the same species, and, second, to designate a group composed of several species. The single species population can be studied from a genetic or qualitative aspect and from a numerical or quantitative aspect. The genetic aspect is concerned primarily with the problem of evolution; with the transmission through the population of a group of genes in certain frequencies. It is only the single-species population that has this attribute. Such a population reproducing by means of biparental inheritance has great material reality since each individual is ultimately linked with its fellow by means of a common germinal bridge. Thus, in a population sense, a species is a vast biological continuum in both time and space.

Both the single-species population and the mixed-species population possess a structural or quantitative aspect which, as ecologists, merits our attention and analysis. We could paraphrase this aspect as the "dynamics of numbers" since the interest centers around census material. For all populations we must have numerical information about matters of density, age and sex. In addi-

tion, for the mixed-population, we must know the kind and number of species comprising the entire group. For both types of populations the general technique of analysis is similar. I see no difficulty in using the word "population" for either intra- or inter-specific aggregations and shall not further labor the point. Let us proceed to an analysis of the five basic questions.

II

Population studies of an analytical nature are being developed primarily along three fronts: studies that might be called statistical; purely experimental approaches, and, investigations combining both techniques. All three methods, although possessing their individual limitations, are contributing valuable material to the general program.

This is not the place, nor am I the person, to summarize critically the work conducted by the population statisticians. Important contributions have been made by Lotka, Pearl, Volterra, Wright, Nicholson and others. It is necessary for the general emphasis of this paper, however, to attempt a brief survey of the interests of these workers since their ideas and concepts are relatable to our own discussion.

The mathematical work in the ecological population field appears to fall into three categories: the use of statistical methods, the development of empirical curves to describe the growth of populations and the rationalization of equations that picture inter-species competition. Statistical methods have already been disposed of by stressing the fact that population phenomena are group problems and patently must be handled biometrically. The empirical work has centered about the fitting of mathematical functions to demonstrated population facts. The best known and most useful study in this connection has been the development and extension of the Logistic Curve by Pearl and Reed. More will be said about the application of this work later. The third group of workers, exemplified by Lotka and Volterra, have attempted to derive equations that express competition between the population components when certain assumptions regarding such factors as natality and mortality, food supply and effective population size are postulated. This work stems back to the epidemiological studies of Ross who in 1908 showed mathematically that the incidence of malaria in a limited area could be predicted if certain facts were known about the human and *Plasmodium* populations in that area. Ross's results were of little practical or immediate biological significance due to their extreme oversimplification. They did aid, however, in delineating a field for further analysis.

This analysis has been principally carried on by Volterra and Lotka. They have developed, among others, a series of equations that describe the interaction of associated organisms when two species are competing for the same food and when two species exist in a predator-prey relationship. The conclusions they reach are both interesting and polemic as I think all of us would grant. However, as biologists we are interested in knowing: do the equations depict a natural series of events, or, are they merely superb mental exercises?

In short, do they *work?* At the moment only an evasive yes-and-no can be given in answer to this question. We shall return to the point in discussing the contribution of these studies to general ecology.

Students interested in the experimental biology of populations have worked largely within a single species. Their interests have centered about two problems: (1) the description of population *trends;* that is, the nature of the growth, maintenance, oscillation and decline of a population under laboratory conditions, and (2) the *dynamics* of population trends or a study of those factors that control the characteristic growth pattern. The former work is important in that it provides what might be called the basic descriptive data. The later work aids in an understanding of the mechanics. The factor most intensively analyzed in population studies has been the nature and action of population density. The emphasis concentrated here has not been misdirected. One of the very unique properties of a population is the fact that the density created by the component organisms changes with time. There is considerable evidence to indicate that these changes frequently play a causative role in shaping population trends. In studying the density problem, population biologists have most frequently analyzed the effect of crowding upon the statistical consequences of reproduction (the birth-rate) and upon the statistical consequences of mortality (the death-rate). It has been said, and pregnantly, that all population and evolutionary phenomena are ultimately grounded in the quantitative relation of births to deaths.

The third important frontier along which investigators are attacking the population problem combines the mathematical with the experimental method. This is a new field and promises to contribute much to our knowledge of population mechanics. It is being chiefly exploited by the Russian biologist Gause in his studies on the inter-species competition problem and merits a more detailed discussion later. The essential idea behind work of this type is to start with an equation that rationalizes a certain situation between two mingling populations, say a predator-prey relationship, and then attempt to corroborate the predictions of the equation with actual laboratory material. Under this system the investigator is guided in the construction and control of his experiment by the postulates inherent in the mathematical system. If the results materialize as the mathematics demand the latter may be considered vindicated. If they do not so turn out the investigator must look to new experiments and seek solace in the so-called "Harvard Law"[2] of animal behavior.

III

The foregoing remarks have dealt somewhat briefly with the points of attack and methods in present use by the population biologists. We are now ready for a consideration of some of the experimental investigations in the population field along with certain concepts that have emerged from this work.

2. The "Harvard Law" of Animal Behavior which I have heard through tradition and not through publication states that, ". . . . animals under the most precisely controlled laboratory conditions do as they damn please."

It appears to me that the most significant results fall into two main categories: the logistic nature of the growth of populations and studies that throw light on the action of density.

The logistic curve has had an interesting history and development. It first appears in the literature in 1844 when a Belgian mathematician, Verhulst, showed it to be an adequate description of growth phenomena. Later (1920) the curve was independently rediscovered and extended by Pearl and Reed who demonstrated that it could be used in fitting the growth of a variety of populations. To date a series of growth relationships have been expressed in terms of the logistic curve. Among these are the increase in weight of individual pumpkins (Cucurbita) and individual male white rats; the growth of laboratory cultures of yeast, *Paramecium*, *Drosophila*, and *Tribolium*, as well as the growth of human populations. The latter have been dealt with as districts, cities, states, countries and world units. In essentially all cases the graduation of the curve to the actual data is remarkably close.

Taking it for granted that the logistic curve is a good description of quantitative increase what biological facts and suggestions can be deduced from the study of the curve? Inherent in the curve are the following properties of significance in an analysis of population growth (Pearl, 1924):

1. The area upon which the population grows is a finite area with definite limits, however large.

2. The number of individuals (population density) that can be supported in a specified area is limited; in other words, the asymptote of the curve approaches a finite number.

3. The lower asymptote of the curve is zero; negative populations are unimaginable.

4. Population growth may be cyclical in character with new logistic cycles additive. Adaptive changes between the population and its environment may initiate a new cycle of growth superimposed on the other one. For example, the agricultural stage of human culture supported higher population densities than did the pastoral stage.

5. The general shape of the curve shows that populations possess, first, a slow rate of growth; second, the rate increases until it reaches a maximum (the inflection point of the curve), and third, the rate becomes progressively less until the curve stretches out nearly horizontally in close approach to the upper asymptote.

The differential equation from which the logistic curve is derived is

$$\frac{dN}{dt} = bN\,\frac{K-N}{K}$$

where b is the maximum potential rate of reproduction for each organism in the population; N is the total population size at any moment of growth; t is time or age, and K is the maximal population possible under the obtaining ecological conditions. This equation (see Gause, 1934) can be stated in words as follows:

$$\left\{\begin{matrix}\text{The rate of population}\\ \text{growth.}\end{matrix}\right\} = \left\{\begin{matrix}\text{The potential increase}\\ \text{of the population per}\\ \text{unit of time.}\end{matrix}\right\} \times \left\{\begin{matrix}\text{The degree of reali-}\\ \text{zation of the potential}\\ \text{increase.}\end{matrix}\right\}$$

The rationalization of the logistic curve becomes more tangible and relates more directly to biological variables if it is applied to an actual case. Gause

(1934) has done this for the growth of populations of *Paramecium caudatum*. In this work five individual infusorians were placed in 0.5 cubic centimeter of nutritive medium. The experiment was replicated and counts of organisms were made at 24 hour intervals for six days. When fitted to a logistic curve the actual growth data were shown to correspond closely to the curve itself. This is seen in Figure 1 where age of the culture in days is plotted on the

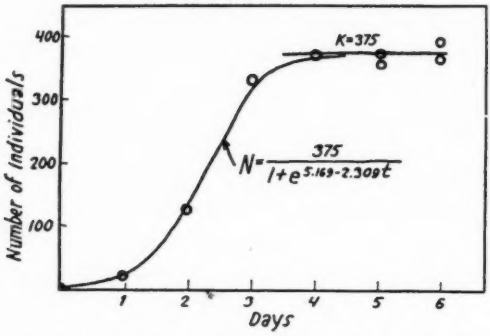


Fig. 1. The logistic growth of a population of *Paramecium caudatum*. (From Gause, "The Struggle for Existence." Courtesy of the author and the Williams & Wilkins Company.)

abscissa and total population size appears on the ordinate. The graph describes a population *trend*. The interesting feature of the study is that something can be deduced about the dynamic factors involved in the growth of this particular population by assuming that the population is growing as the curve suggests and then calculating certain parameters from the curve equation. As Gause puts it we are interested in the following question: ". . . what is the potential rate of increase of *Paramecium* under our conditions, and how does it become reduced in the process of growth as the environmental resistance increases?"

From inspection of the curve it can be seen that the maximal population possible under the respective conditions is 375 Paramecia per 0.5 cubic centimeter of medium. This is the value, K. In fitting the curve, b, or the rate of reproduction was found to be 2.309. This means that for a 24 hour period every individual protozoan can potentially produce 2.309 others. Knowing these two values Gause was able to compute certain other expressions of population importance. These are summarized in Table 1. The first line shows the change in number of organisms during the initial four days of growth. The population increases from 20.4 individuals to 137.2, to 319.0 to 369.0. If the ecological conditions are not altered N remains around 369. The second line of the table expresses the potential increase of the population per day or the number of offspring which a given population of *Paramecium* can potentially produce within 24 hours. This is a geometric increase and is not actually

TABLE 1

The growth of a population of *Paramecium caudatum* (Gause, 1934) b(coefficient of multiplication; potential progeny per individual per day) = 2.309 K(maximal population) = 375.

	Time in Days			
	1	2	3	4
N (number of individuals according to Logistic Curve)	20.4	137.2	319.0	369.0
bN (potential increase of the population per day)	47.1	316.8	736.6	852.0
$\frac{K-N}{K}$ (degree of realization of the potential increase)	0.945	0.633	0.149	0.016
$1-\frac{K-N}{K}$ (environmental resistance)	0.055	0.376	0.851	0.984
$\frac{dN}{dt} = bN\frac{K-N}{K}$ (rate of population growth)	44.5	200.0	109.7	13.6

realized in the population. The extent of realization is indicated by the ratio $\frac{K-N}{K}$ which approaches one on the first day when the potential growth is nearly entirely realized and is reduced to 0.016 on the fourth day when very few additional Paramecia are added to the already existing total. The reason the potential increase becomes successively lower as the population grows is due to the fact that the environmental resistance becomes increasingly severe. Gause expresses this resistance as $1 - \frac{K-N}{K}$; a reciprocal of the realization of the potential increase. The table shows the environmental resistance is low in early stages of population growth and high at the time the growth has approached its asymptote. The last entry in the table represents the rate of growth of the population and is merely the arithmetical solution of the logistic curve. The figures show that the population grows rapidly between the first and second day after which the rate of increase slackens. For example, 44.5 individuals are added to the culture during the first 24 hours; 200.0 during the second 24 hours; 109.7 during the third, and 13.6 during the fourth.

Gause designates the relationships we have been discussing as "characteristics of competition" and has illustrated them graphically. Figure 2 depicts on a relative scale the operation of certain factors within a population of *Paramecium caudatum*. This drawing adds nothing to that already said but may be of assistance in summarizing succinctly the material presented.

Enough time has been given to the logistic curve. I have tried to show (1) that it does, in most cases, give a good description of population growth;

(2) that it directs attention to certain general factors which play a causative role in population trends and permits these factors to be arithmetically appraised, and, (3) that, while the logistic curve does not indicate what these factors are biologically, it does emphasize their existence and recommend further experimentation. I think the logistic curve is a valuable demographic tool when not over-interpreted and when used intelligently as an empirical record of population growth.

The general subject that has interested the experimental population student is the analysis of population density. As mentioned earlier this is a justifiable emphasis. Several biologists (see Pearl, 1930; Allee, 1931; Park, 1937) have pointed out that the effects associated with the number of organisms present in a group are among the most significant biological, as contrasted to the physical, elements of the environment.

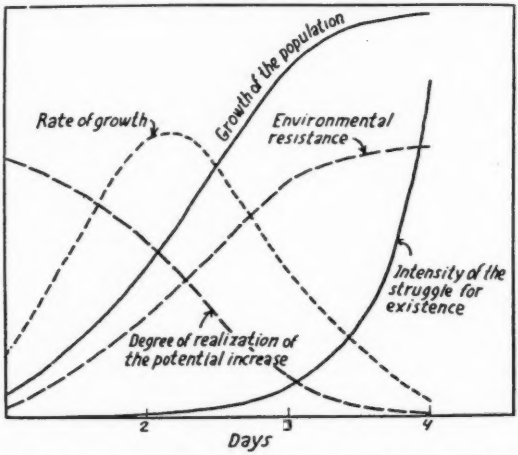


Fig. 2. Graphical representation of competition in a homogeneous population of *Paramecium caudatum*. (From Gause, "The Struggle for Existence." Courtesy of the author and the Williams & Wilkins Company.)

The analyses of population density can be divided into three arbitrary categories: first, the kinds of processes and events that have been shown to be influenced by density; second, the type of end results induced by density irrespective of the process involved, and, third, the nature and constitution of density *per se*.

In reviewing the first category it is only necessary to present a partially complete list to make the point that the crowding of organisms within a limited environment can elicit a number of diverse responses on the part of the component organisms themselves. The following events have been shown to be influenced by population density; rate of reproduction, mortality, the post-

embryonic development of insects, the growth of individual organisms, oxygen-consumption, protection from environmental poisons, resistance of marine forms to hypotonic seawater and to other unusual physical conditions, communal activity of bacteria and spermatozoa, the determination of sex, and certain morphological expressions such as the development of wings by aphids and the initiation of new color phases by locusts. Patently, not all these events are of immediate importance in the biology of populations. The major point in presenting this list is to emphasize that, whether in the laboratory or under natural conditions, populations exert, as a result of their own uniqueness, varied effects upon their constituents. There is not the time, nor is it particularly relevant to our topic, to pursue this point further. For additional information the general writings of Allee (1931, 1934, 1938) can be cordially recommended.

We are more directly interested in the second part of our review—the type of end effects induced by density. This is a subject pertinent both to population dynamics and ecological theory. It long has been recognized that the increased crowding of organisms in a population reduces the population growth rate. This view has been held for both laboratory and human populations. As early as 1843 Farr developed an equation that expressed an inverse ratio between crowding and human mortality. There have been many experimental reports that corroborate findings of this sort and the conclusion seems inescapable that increased population density is frequently an inhibitor of population growth. We shall review some evidence for this statement and relate the concept to ecological theory.

However, this is not the whole story. There is rapidly accumulating a respectable body of data suggesting that crowding, under specified conditions, may be stimulating to population growth. We are indebted mainly to Allee for clearly stating and delineating this aspect of the problem. He has marshalled many facts in support of the concept that "undercrowding," as well as "overcrowding" may contribute to population decline.

A better appreciation of the two types of crowding effects can be got by examining analyses that illustrate both. Numerous excellent studies could be chosen on either side. I think the effect of population density on the reproduction of *Drosophila melanogaster* will serve as a good example of the overcrowding type and the so-called "allelocatalytic" effect exhibited by microörganisms as interesting example of the retarding effects of undercrowding. Both these studies yield data pertinent to population problems and general ecology.

The Drosophila situation has been worked out primarily by Pearl and his associates (Pearl and Parker, 1922; Pearl, 1932). In their initial experiments they set up populations of flies at densities ranging from one pair per half-pint bottle to fifty pairs per half-pint bottle and counted the progeny produced by the different cultures. Their data showed that as the population density increased the number of offspring per bottle decreased. In other words, productivity stood in inverse proportion to population density. Since only the

imago progeny were counted this work did not demonstrate what physiological process was being inhibited to bring about the described result. Density could be operating by reducing the rate of oviposition or fecundity of the flies, by lowering the fertility of the eggs once laid, by adversely affecting the metamorphosis of the flies in crowded cultures or by any combination of the three effects.

To get at these questions a technique was developed by which eggs could be observed and counted. Experiments were started in which the initial densities varied in a geometric series from one to 128 pairs of Drosophila per standard bottle. The eggs were collected at regular intervals from each container and counted. It was shown that the fecundity was greatly inhibited by the crowding of imago flies in the bottle, since the oviposition, expressed as a rate per female per day, fell off rapidly as the density increased. No important relations between density and fertility or metamorphosis were reported. From this analysis there emerges, first, the fact that overcrowding in *Drosophila* is harmful to population growth, and, second, the demonstration that reduced growth in crowded populations is attributable primarily to a lowering of the rate of oviposition. Pearl also made an intensive study of the way in which density was reducing fecundity. This will be considered later.

This *Drosophila* situation will serve as an example of the numerous cases where overcrowding is associated with a general retardation. The case is of particular significance for us since the retardation described here, reduction of the birth-rate, is immediately concerned with a population response. Not all the effects induced by overcrowding have population or ecologic significance.

Frequently in populations the optimal density is greater than the smallest possible density. In these situations, "undercrowding," to use Allee's term, becomes as important as "overcrowding." One of the most interesting developments along this line has been the demonstration of the so-called allelocatalytic effect among protozoa. This work is interesting technically and biologically as I will attempt to show. It is also entertaining historically for it demonstrates admirably how one report, whether right or wrong, can stimulate a long line of productive and provocative research. I can not take time to review this matter in detail; I only hope to present briefly the high points.

In 1921 T. B. Robertson published a report on the population growth rate of two ciliate protozoans, *Enchelys* and *Colpoda*. He found that when either of these two forms was introduced into a small volume of fresh culture medium the fission rate per organism was increased by a certain amount of crowding. Specifically, two infusoria in the same environment reproduced from 2.5 to 10 times as fast as did isolated forms. This difference, when tested with appropriate statistical methods, was a larger one than could be anticipated on chance operation alone. Robertson called these events and their interpretation, "allelocatalysis." We shall carefully distinguish between the *facts* of allelocatalysis just outlined and the *theory* to follow. In explaining his results Robertson hypothesized

> .... during nuclear division each nucleus retains the charge of autocatalyst with

which it was provided, and adds to it during the course of nuclear synthesis. At each division the autocatalyst is shared between the nuclear substance and the surrounding medium in a proportion determined by its relative solubility and by its affinity for chemical substances within the nucleus. The mutually accelerated or allelocatalytic effect of contiguous cells is due to each cell's losing less of the autocatalyst to the medium because of the presence of the other. (Allee, 1931, p. 166).

The evidence in favor of the allelocatalytic theory seemed feeble. Whether for this cause or another a number of investigators started working along similar lines using various ciliate and flagellate species. Most of the workers reported negative results; that is, data showing that the isolated organisms reproduced as fast or faster than the grouped organisms. None of the workers seemed particularly attracted to the theoretical explanation; especially so since they had little confidence in the existence of the phenomenon. This went on for about five years until Yocum in 1928 reported results with *Oxytricha* which he interpreted as allelocatalysis. He found that the rate of fission of infusorians cultured singly in four-drop cultures was 10 percent greater after 24 hours than that of single forms in ten-drop cultures. In other words, by reducing the volume the reproductive rate had been stimulated.

During the next year Petersen (1929) obtained results with *Paramecium* that straddled the academic fence. If she used a small volume of medium there was no difference in fission rate between single and grouped organisms. In a larger volume of medium, however, the latter divided significantly faster than did the former. This work is important in that it showed for the first time that the effect could be produced at will by the manipulation of a known experimental variable. Petersen did not subscribe to the explanation of Robertson.

An important contribution on the positive side was made by Johnson in 1933 using *Oxytricha*. He first confirmed Petersen's results about the effect of volume of medium on division rate and then proceeded to analyze what factors were involved in these volume relationships. In sum, Johnson showed that the bacterial flora of the cultures is important in controlling the fission rate of the organism. He first set up a series of cultures in which the bacterial population varied from a high to a low concentration and introduced a single infusorian into each culture. Under these conditions the fission rate was significantly highest in the intermediate bacterial concentrations and fell off as the bacterial crowding got either greater or smaller. This is cogent evidence for the existence of an optimal bacterial density for maximal reproduction of *Oxytricha*. Johnson further showed that if he introduced paired, as well as single, organisms into the series of bacterial concentrations the former reproduced faster in the supra-optimal densities. This is probably due to the fact that the paired *Oxytricha* can control and reduce, during early population growth, the bacteria more efficiently than can the isolated forms.

This investigation again fails to corroborate the allelocatalytic theory but does show that Robertson's results are actually possible experimentally. The

.... work leaves unsolved the question of the relative importance of bacterial as opposed to some other sort of biological conditioning through the production of excre-

tory matter or of some X-substance. It does indicate that the introduction of a second infusorian may reduce the supraoptimal numbers of bacteria towards the optimum; that the introduced protozoan may introduce more suitable bacteria, or less suitable ones; in short, the work has made it necessary that in future experimental attacks on the problem the bacterial flora shall be under control. (Allee, 1934, p. 18).

Two interesting affirmative reports on the subject are appearing this year (1938). One, a paper on the soil amoeba, *Mayorella,* by Reich (1938) is currently in press. The second, has appeared as an abstract by Mast and Pace (1938). Reich has shown that when amoebae are grown as mass cultures free of bacteria those with small initial populations have a lower division rate than do those with larger initial populations. These results clearly confirm the general effect but are apt to elicit a certain perplexity since they have been obtained presumably in the complete absence of bacteria and since they offer no explanation or interpretation of the phenomenon whatsoever.

The final touch to the whole story is added by the work of Mast and Pace dealing with the flagellate, *Chilomonas*. This form can be cultured in a sterile solution containing only relatively simple chemicals in known proportions and thus is admirably suited for growth studies. The experiments were set up so that density and volume relations were varied and the rate of multiplication was assayed. According to the abstract the data ". . . . prove conclusively that, within certain limits, as the numbers of chilomonads per volume of solution increases, the frequency of fission increases, to a maximum of more than 50 percent, then decreases to zero." The authors feel that their results ". . . . strongly indicate that *Chilomonas* secretes a substance which favors growth."

Thus the problem stands after eighteen years of active research in many laboratories. First, a phenomenon and theoretical interpretation was presented; then, there came a long series of reports not confirming the phenomenon; then, a few observations substantiating the phenomenon but not accepting the theory; then, further substantiation of the fact with evidence for a cause of a different nature; then, substantiation of the fact with rejection of the new interpretation and, finally, a substantiation with an interpretation rather like the original in general biological nature! The "Robertson effect" has been useful for our purposes because it provides a lively example of the concept that undercrowding can be as deleterious from a population viewpoint as overcrowding. It is also good evidence for the hypothesis that the history of an idea is cyclical in character.

Having demonstrated first, that crowding elicits many physiological and morphological responses, and, second, that these responses are frequently of causal importance in the biology of the population, the population student next turns his attention to the analysis of the factors that comprise and give reality to the density concept. Population density can be defined in purely physical terms as the number of individual organisms per unit of space. Biologically, this is a sterile definition. It is useful only in the sense that it gives us a statistical expression of size. Contrariwise, I think there is some danger

in thinking first-hand of population density in purely "psychological" terms; in attributing the ultimate cause of the observed effect to some subtle interaction that emerges purely from the uniqueness of the number relationships. This may lead to a certain mysticism. There may, of course, be situations, as in human groups, where such an explanation is the legitimate one. The aim of the experimentalist is to dissect density into tangible components if possible before resorting to a more intangible substitute.

Experimental analyses, particularly of insect populations, are showing that density usually operates in one or two ways. In some cases, it is the action of the organisms upon each other in a behavioristic fashion which is responsible for the observed result. In other cases, density may be broken down into different units and shown to be acting through such secondary effects as the reduction of the available food supply, the charging of the medium with waste-products and other modifications of the environment. Indubitably, in all natural populations where the actual numbers of organisms are not experimentally divorced from such alterations of the environment, both types of effects are operative, though not necessarily to an equal degree.

The *Drosophila* experiments earlier discussed offer an interesting picture of density operating through a behavior mechanism. It will be recalled that Pearl demonstrated that the egg-production of female flies was reduced as the crowding increased. In analyzing this situation experiments were set up that varied the air volume in the bottles in the presence of initial densities that ranged from one to 128 paired *Drosophila*. The eggs were counted at 24 hour intervals. It was found that, while the extent of the air space above the culture medium had no significant effect on oviposition, the extent of crowding of the flies on the agar surface was highly important in altering their fecundity. To put it differently, the real density effect occurs when the flies are crowded together on this agar surface. By making a careful series of observations on the behavior of crowded and isolated flies Pearl concluded that *Drosophila* will not oviposit if they are in contact with or disturbed by other flies, and that individual flies do not obtain as much food under such conditions even though there is an ample supply of food present for their consumption. This was called the "interference" or "collision" effect and it was shown that the probability of collisions between *Drosophila* on the agar surface of the medium increased with density and followed a random pattern. The investigation thus links the population effect, through fecundity, to two *behavior* mechanisms—the inability of *Drosophila* to oviposit and feed adequately when disturbed by their own culture mates.

I have been concerned for some years with the population biology of the flour beetle, *Tribolium confusum* (Park, 1934). Chapman (1928) in his interesting paper on biotic potential, pointed out the adaptability of this species for synecological studies. In the last decade a number of reports have appeared that could be reviewed this evening. However, since my time is limited I wish to mention briefly some work (Park, 1938) with *Tribolium*

that illustrates a density effect operating primarily through alteration of the environment. If *Tribolium* populations are allowed to age without disturbing the flour in which they live, the cultures gradually become extinct and the flour noticeably changes in chemical and physical composition. I speak of this change in the medium as biological conditioning. "Conditioned flour" represents a substance which is produced by the beetles in their normal course of living. It is an inevitable product of population activity owing its existence entirely to the cumulative effects of the breeding and general behavior of the beetles themselves. More specifically, conditioned flour differs from fresh or unconditioned flour in that the beetles inhabiting it have reduced its nutritive value through constant feeding and have added certain by-products such as execretory and metabolic wastes not present in the original medium.

A series of investigations on the conditioned flour problem (for summary see Park and Woollcott, 1937) have shown that *Tribolium* has a number of its activities inhibited when living in such an environment. For example, the fecundity of the beetles is drastically reduced by this treatment. Recent studies (Park, 1938) have analyzed the relation of environmental conditioning to the "efficiency" of *Tribolium* metamorphosis. Efficiency was measured by studying as groups the duration and mortality of the larval and pupal periods. In setting up the experiments two series of densities, ranging from 1 to 256 larvae per bottle, were established. All densities were started in four grams of fresh flour. Each bottle was examined at 48 hour intervals and deaths were recorded. Series I did not have the flour replaced at any time during the metamorphic period. In Series II the flour was completely renewed at the time of examination—that is, every other day. Thus Series I and II are identical in all particulars except type of medium. The results are quite clear-cut. The Series I group had its larval and pupal mortality increased and the rate of larval development strikingly decreased as the population densities got larger. The Series II group was essentially unaffected by density relationships. This means that, by and large, a larva reared with, say, 127 others had just as much chance of living and passing rapidly through its development as one reared in isolation.

The data may be interpreted in this fashion. In each series an extensive and identical density differential exists. In Series I this differential is highly correlated with increased mortality and reduced rate of metamorphosis. In Series II this is not the case. The only known difference existing between the two series is that in the first one the medium was not changed. In other words, the flour became cumulatively more conditioned with age and crowding. The 256 density culture conditioned its environment at a much faster rate than the 128 culture, which in turn induced more conditioning than the 64, and so on. In the second series the flour was experimentally prevented from becoming conditioned to any degree. It is patent that the major density effect is a conditioning effect working, not through the behavioristic interaction of the larvae since this is identical for both series, but through the mass influence these larvae exert on their environment. It seems to me the effect is none the less real for this reason.

IV

Earlier in this discussion I mentioned the work of the population mathematicians and pointed out, as the third line of attack, that certain schools were combining this technique with the experimental method. This report would not be complete if such studies were overlooked. A very instructive analysis in this connection is Gause's (1934) discussion of the predator-prey type of population competition. Lotka and Volterra have developed equations that describe the struggle for existence when two species, one a predator, the other the prey, inhabit the same microcosm. These equations lead to the prediction that the number of prey and predators will fluctuate in definite cycles of abundance and sparseness due to innate properties of the biological system not related to external environmental forces. The story, as described by the mathematicians, runs something like this: if, in a limited environment we have N_1 number of prey, and, if an N_2 number of predators are introduced into the system, the concentration of the prey diminishes and that of the predators increases. However, as the predators increase they devour more and more of the prey so that the latter become fewer in number. This creates a food shortage for the predators and most of them die off. As a result the pressure on the prey is relieved and they increase rapidly, soon becoming the dominant species. The few predators which did survive the food shortage now flourish and multiply abundantly. Thus the cycle is reconstituted.

Gause is interested in seeing if these "classical" oscillations of predators and prey, predicted on a stochastic basis, can be realized by experimental data. To get at this he chose two infusoria which live under similar ecological conditions: *Didinium* and *Paramecium*, the predator and the prey respectively. The former species requires for its nutriment a fresh *Paramecium* every three hours. The bacterium, *Bacillus pyocyaneus*, was always present in the medium of this and subsequent experiments to supply the Paramecia with food. In the first experiment five Paramecia were placed in a clear oaten medium and two days later three of the preying *Didinium* were added. After the introduction of the predators the number of Paramecia decrease, the *Didinium* multiply, intensively devour all the prey, and then starve to death. Clearly this experiment offers no support to the predictions of the mathematicians and furnishes no evidence of an innate periodic oscillation of numbers for such a system. Gause has this interesting observation to make:

> However, why is the theoretical equation of the mathematicians not realized in our case? The cause of this is apparently that a purely biological property of our predator has not been taken into account in the equation. According to this equation a decrease in the concentration of the prey diminishes the probability of their encounters with the predators, and causes a sharp decrease in the multiplication of the latter, and afterwards this even leads to their partly dying out. However, in the actual case *Didinium* in spite of the insufficiency of food continues to multiply intensely at the expense of a vast decrease in size of the individual.

This matter was tested further experimentally by slightly changing the medium in order that some of the Paramecia could escape from the *Didinium*. The experiment was developed on the grounds that the more heterogenous

environment simulated the natural conditions more closely. The change was brought about by using a medium containing a sediment in which the prey was free to go but which barred all the predators. Under these conditions all the *Didinium* would be found in the clear part of the medium and the *Paramecium* would be moving in and out of the sedimentary deposits. In short, the system provides the prey with a "refuge." For the majority of cases the results of this experiment were clear-cut. If *Paramecium* and *Didinium* are simultaneously introduced into the microcosm the latter increase somewhat and devour some of the Paramecia. A considerable group of the prey, however, escape into the sediment and there can not be attacked. The *Didinium* soon eat all the Paramecia in the clear part of the medium and then starve. In the meantime, the sequestered Paramecia have multiplied greatly and soon the culture becomes entirely composed of this species. Here again, under presumably more "natural" conditions, the "classical" results do not obtain.

In his third group of experiments Doctor Gause uses the clear oaten medium and at the beginning and every third day thereafter added one *Paramecium* and one *Didinium* to the culture. Under these conditions an actual experimental oscillation of the predators and prey was demonstrable with first the *Paramecia* being most numerous and then the *Didinium*. The author's final word on the matter is,

> The above given example shows that in *Paramecium* and *Didinium* the periodic oscillations in the numbers of the predators and of the prey are not a property of the predator-prey interaction itself, as the mathematicians suspected, but apparently occur as a result of constant interferences from without in the development of this interaction. There is evidence for believing that this is characteristic for more than one special case.

V

Ecology appears to stand in great need of coördination and synthesis. That the field has produced an abundance of factual material in the last thirty years is indisputable. However, the facts have not been adequately assembled into principles and concepts (Allee and Park, 1937). The material I have just reviewed should, I hope, make the point that population studies, as a branch of general biology, are yielding facts and some ideas of ecologic value. I do not mean to imply that these studies are panaceas for the ills of ecology; I only suggest that they have something to contribute to an understanding of the natural population. It is true that communities of organisms in nature are more complex than experimental laboratory cultures. They are both, however, subject in final analysis to similar controlling factors. Reproduction and mortality, density relationships, competitions of various kinds and reactions to elements of the physical environment are common to both groups. The experimental population student makes his major contribution when he is able to give reality and precision to these factors. The contribution becomes greater when the field biologist can take over such results and apply them, both as techniques and as concepts, to his own province.

More specifically, what are some of the contributions that analytical population studies have to offer for community ecology? In looking back over the work discussed this evening the major contributions appear to be two: method-

ological and conceptual. In terms of methods we have emphasized that ecology is, to a large degree, a quantitative science: the ultimate problems are group and group-interaction problems. To get at such interactions we must employ quantitative methods. Population studies are showing how this may be done in the laboratory.

The population mathematicians should be able to contribute along both methodological and conceptual lines. To date they have not added much material of tangible value to community analysis. This is attributable to the fact that their concern has been, of necessity, with over-simplified situations. There is the added difficulty that most of us are unprepared to work in such rarified mathematical niches even if so disposed. However, I am still quite optimistic about the role of these studies in the future development of synecology. I do not feel that the results will go far if divorced from empirical findings but when the two are used in conjunction the end product should be stimulating. The general worth of these studies is that they focus attention on competition; not as a disparate phenomenon but as an orderly series of group events. This will prove important in community studies and may also serve the added purpose of drawing the ecologist into the investigation of problems of evolution and speciation. It seems lamentable that the ecologists have not joined with the geneticists in actively exploring a field that is no more the bailiwick of one than the other.

The mathematical studies have raised such questions as these. It would be interesting, for example, if we knew that communities grew according to the logistic curve, and, if we had additional information about the cyclic fluctuations in numbers exhibited by the community components. Interesting, because a description of events would exist and because there would be some suggestion as to the causes of those events. Such results would aid in ordering community dynamics. I do not think this is too much to hope for. As far as the logistic curve is concerned we already know that it fits the growth of many populations including the complex human situation. Also, there are indications that many cycles in nature are amenable to close quantitative description. The Scandinavian school of animal ecologists are actively working along lines that combine mathematical, experimental and field techniques as applied to fisheries problems. A number of the sounder economic zoölogists, interested in questions of biological control, are turning to such combinations. We, as ecologists, will find this work well worth following because of its application to natural population problems.

Probably the most important ecological contributions, however, have emerged from the experimental studies; particularly the analyses of density. Population density is not purely a phenomenon created by laboratory conditions. In a beech-maple forest organisms are competing for space just as are *Tribolium* beetles in a culture of flour. As we have seen the experimental studies have (1) given biological reality and meaning to density; (2) demonstrated the variety of organismic processes subject to its influence; (3) shown that the end results of increased crowding may be either immediately inhibiting or else stimulating to the population, and (4) suggested that density operates through behavioristic and environmental channels.

This detailed knowledge is applicable to community analysis. It is obviously important to know that the crowding of forms in their respective niches affects such processes as reproduction, mortality, rate of metabolism, and so on. Of especial interest are the studies showing the density differentials may play an inhibiting or stimulating role in the community. The effects of excess crowding, exemplified experimentally by the *Drosophila* situation, are well appreciated by most ecologists who are aware that overpopulation in nature destroys community balance and may result in anything from a slight food shortage or shift in numbers to explosive mass migrations or disease pandemics. Taking a long time view of the community the effects engendered by overcrowding may not be deleterious since they might lead to a new and more favorable adjustment between population and environment. Thus I think it not a good plan to speak of overcrowding as "harmful" or, for that matter, optimal crowding as "beneficial."

There is another side to the story. Organisms frequently aggregate in nature and, by increasing their density, effectively improve their immediate conditions. Such natural aggregations are common occurrences and lead to the important principle of "coöperation." The coöperation concept has been generally recognized for a long time. It is inherent in the old "web of life" chestnut and appears in the writings of Forbes and Möbius. In a sense it is complementary to the "struggle for existence" which usually connotes that overcrowding and struggle go hand-in-hand. We are indebted to Allee, however, for giving modern meaning to the principle of unconscious coöperation. He has shown that organsms, both in the field and in the laboratory, frequently better their existence through their mutual presence. This is an important factor to account for when viewing the integration of the biocoenosis. It is a concept developed largely from population research. Allee has also thought these aggregations were the precursors of social origins. I do not think this point of view can be considered proved as yet although the data in its favor are certainly suggestive.

In showing that population density operates through behavior and environmental effects the point is made that these factors must be examined in detail in the natural population. A study of the interactions between the component organisms and the modifications these organisms impose on their environment are essential emphases of community analysis.

In concluding, let us grant that the analytical population student and the field ecologist should coöperate. On the basis of their coöperation what are some common grounds of mutual concern? There are, of course, many; I think four promising lines of attack are,

1. The acquiring of more basic facts about population *trends* both in respect of laboratory and field populations.

2. Further analyses designed to see if theoretical frameworks of population interactions can be made more universal and understandable without loss of basic simplicity.

3. The empirical fitting of these frameworks with actual material as a test of their worth.

4. Closer analysis and understanding of the relations, common properties and differences between the experimental and the natural population.

REFERENCES

ALLEE, W. C. 1931—Animal Aggregations: A study in general sociology. Chicago. University of Chicago Press. 431 pp.

———1934—Recent studies in mass physiology. Biol. Reviews **9**:1-48.

———1938—The social life of animals. New York, Norton. 288 pp.

——— AND THOMAS PARK. 1937—Concerning ecological principles. (abstract) Bull. Ecol. Soc. Amer. **18**: (December).

CHAPMAN, R. N. 1928—The quantitative analysis of environmental factors. Ecology **9**:111-122.

FARR, WILLIAM. 1843—Causes of the high mortality in town districts. 5th Annual Rept. Reg. Gen. of Births, Deaths and Marriages in England, (2nd. ed), pp. 406-435.

GAUSE, G. F. 1934—The struggle for existence. Baltimore, Williams & Wilkins. 163 pp.

JOHNSON, W. H. 1933—Effects of population density on the rate of reproduction in *Oxytricha*. Physiol. Zool. **6**:22-54.

MAST, S. O. AND D. M. PACE. 1937—The relation between the number of individuals per volume of culture solution and the rate of growth in *Chilomonas paramecium*. (abstract) Anat. Rec. **70**(supplement 1):40.

PARK, THOMAS. 1934—Observations on the general biology of the flour beetle, *Tribolium confusum*. Quart. Rev. Biol. **9**:36-54.

———1937—Experimental studies of insect populations. Amer. Nat. **71**:21-33.

———1938—Studies in population physiology. viii. The effect of larval population density on the post-embryonic development of the flour beetle, *Tribolium confusum*. J. Expt. Zool. **79**:51-70.

———AND NANCY WOOLLCOTT. 1937—Studies in population physiology. vii. The relatiion of environmental conditioning to the decline of *Tribolium confusum* populations. Physiol. Zool. **10**:197-211.

PEARL, RAYMOND. 1924—Studies in human biology. Baltimore, Williams & Williams, 653 pp.

———1930—The biology of population growth. New York, Knopf. 260 pp.

———1932—The influence of density of population upon egg production in *Drosophila melanogaster*. J. Expt. Zool. **63**:57-84.

———1937—On biological principles affecting populations: human and other. Amer. Nat. **71**:50-68.

———AND L. J. REED. 1920—On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc. Nat. Acad. Sci. **6**:275-288.

———AND S. L. PARKER. 1922—On the influence of density of population upon rate of reproduction in Drosophila. Proc. Nat. Acad. Sci. **8**:212-219.

PETERSON, W. 1929—The relation of density of population to rate of reproduction in *Paramecium caudatum*. Physiol. Zool. **2**:221-254.

REICH, KARL. 1938—Studies in the physiology of Amoeba. ii. The allelocatalytic effect in Amoeba cultures free of bacteria. Physiol. Zool. **11**:347-358.

ROSS, R. 1908—Report on the prevention of malaria in Mauritius.

VERHULST, P. F. 1839—Notice sur la loi que la population suit dans son accroissment. Corr. math. et phys. publ. par A. Quetelet. **10**:113.

YOCUM, H. B. 1928—The effect of the quantity of culture medium on the division rate of *Oxytricha*. Biol. Bull. **54**:410-417.

HULL ZOOLOGICAL LABORATORY,
THE UNIVERSITY OF CHICAGO,
CHICAGO, ILL.

DISCUSSION

Mayr: It seems to me that natural populations were not given as much attention as they deserve. In Mrs. Nice's work on the song sparrow *(Melospiza melodia)* a forty acre tract was studied for seven years, every individual of this population was marked with color bands and thus was known to the author as an individual. The author disproved the occurrence of overcrowding, since special devices such as territory defense prevented it. She also showed that as long as environmental conditions remained stable and constant, there was little fluctuation. The principal result of this study, however, indicates that a good deal of the work done in laboratories applies apparently to special cases only and may lack general validity.

Park: The natural population purposely was not emphasized since my job was to deal with the theoretical and laboratory population. It was not my intention to give equal weight to all provinces of the population problem. With regard to Mrs. Nice's instructive study I do not feel, excellent as it is, that she has observations over a long enough period of time to rule out the possibility of cyclic changes. Both in the field and laboratory, experience is indicating that population density changes with time although the intervals of change may vary from case to case. While there probably are examples of stationary, long-time populations, I think they constitute the exception rather than the rule. I am not greatly alarmed over your suggestion that laboratory population work applies to special cases only. In the first place, I do not think this will prove to be generally true, and, secondly, any information about populations, experimental or other, strikes me as valuable. The modern field is a new one and I think more and more relationship between experimental and field populations will become apparent as work develops.

Emerson: To draw the connection with Mrs. Nice's work for a moment, it would seem to me that, splendid as Mrs. Nice's work is, there still might be population fluctuations over long periods of time which could hardly be expected to be indicated in seven years, but with observations on greater numbers in a longer period of time, might be expressed mathematically.

Park: It is quite probable that eventually population cycles can be expressed mathematically.

Mayr: It is one of the essentials of a complete population analysis to study not only its early development but to study its growth once the population has almost reached an equilibrium. Unless disaster happens to the population, it will run along the final horizontal section of the curve.

Park: The logistic curve is an expression only of population *growth.* It does not bias or influence the description of population changes after the asymptote has been reached. Even though we express population growth logistically we are at complete liberty and in fact do analyze questions of population equilibrium and decline. I do not, however, agree with your statement that the population, barring disaster, will continue in steady equilibrium at the asymptote of the curve. This is a dangerous point to generalize upon without empirical evidence. Many populations oscillate after reaching their maximal size in a fairly predictable fashion. This oscillation is not necessarily about the asymptote although Volterra has suggested ("The Law of Conservation of the Averages") that the *mean* of the cycles tends to be maintained in the absence of marked environmental disturbances.

Discussion of the paper by Thomas Park, "Analytical population studies in relation to general ecology" by Dr. G. F. GAUSE, Research Professor of Experimental Biology, Moscow, U.S.S.R., who participated by invitation.

Those who are accustomed to ponder the development of modern ecology are aware that, although the need for ecological theory is great, the difficulties in obtaining it are equally considerable. Under such circumstances it is hardly possible to disagree with the argument, so admirably developed by the author, that analytical population studies have at least something to offer, with all their restrictions and limitations, to the development of ecological theory. I would like to take this opportunity to say a few words about the following two points: (1) What generalizations and concepts have arisen from analytical population studies and (2) What are some desiderata for population investigations?

One such generalization, which I should like to add to those listed by the author, is that of the regulation in the composition of biotic communities. It has been demonstrated by mathematicians, and strikingly confirmed in experiments with infusorians, that when two or more species have slightly different modes of living, or, in other words, when they occupy different ecological habitat niches, they will live together indefinitely in essentially stable equilibrium. What is more important is the fact that only a certain definite combination between the concentrations of the species living together possesses the property of maintaining stability. Any deviation from this stable combination will automatically, owing to continuous process of competition, lead to the reëstablishment of the steady state. It seems that the central ecological problem of regulation in the composition of complex biotic communities is in these analytical investigations reduced to simplest terms. In the light of all this evidence one may claim that if two or more nearly related species live in the field in a stable association, these species certainly possess different ecological niches. (For further details see Gause, "Verifications expérimentales de la théorie mathématique de la lutte pour la vie", Paris, Hermann, 1935).

Another point, which is particularly significant at the moment, is the need for further population studies. It is certain that the analytical population student and the field ecologist should coöperate, but the useful form of such coöperation should itself be subject to an experimental test. In some cases at least, as it follows from the experience of this laboratory, field investigations raise general problems, sometimes of economic importance, which can be thoroughly analyzed in the laboratory with animals rather remote systematically from those originally studied in the field. It is consequently not the particular animal or group of animals which can be studied both in the field and under simplified laboratory conditions, but only the general ecological situation. To cite but one example from our recent experience, there are two lakes under investigation, in one of which the invertebrate fauna and, consequently, the diet of some economically important species of fish is qualitatively much more diverse than in the other lake. A consideration of the structure of food-chains in these two communities has led to the formulation of a rather general ecological problem, namely that of the behavior of the predator-prey system with different degrees of heterogeneity in the composition of the population of the prey. Variation in numbers and other properties of such systems can be studied analytically with experimental laboratory populations, and there is no doubt that the results of such studies can contribute much towards the explanation of the relations observed in the field. I believe that laboratory ecologists will find in the field many stimulating ecological problems for subsequent analytical study.

Notes and Discussion

Records of Terrestrial Isopoda or Sow Bugs from North America

MELVILLE H. HATCH

The following notes on terrestrial isopods or sow bugs are limited to those species that are purely terrestrial in distribution and, with the possible exception of *Porcellio littorina* Miller, are not confined to the sea-shore. With the exception of *Ligidium gracile* Dana and the species just mentioned, the forms concerned are very probably introduced from Europe, as pointed out by Van Name (Bull. Amer. Mus. Nat. Hist. **71**, 1936, pp. 22, 35-37). But, as Walker (Can. Field Nat. **27**, 1927, pp. 173-179) has shown, though widely distributed, they are very far from being ubiquitous, so that the distributional records here presented are not without significance.

The recognition of the principal species of American sow bugs is not difficult. They may, first of all, be identified with the aid of Harriet Richardson's *Monograph on the Isopods of North America* (Bull. U. S. Nat. Mus. **54**, 1905, 727 pp.). Walker (loc. cit., pp. 173-179) gives a key to the terrestrial species, and Miller (Univ. Calif. Publ. Zool. **43**, 1938, pp. 115-116) gives a key to the terrestrial species of California. They can, moreover, be named by means of the information given by Kunkel's *Arthrostraca of Connecticut* (Conn. St. Geol. Nat. Hist. Surv. Bull. **26**, 1918, pp. 185-254) and by Van Name's *American Land and Fresh-water Isopod Crustacea* (Bull. Amer. Mus. Nat. Hist. **71**, 1936, 535 pp.), and most of them are included in Pratt's *Manual of Common Invertebrate Animals* ed. 1, 1916, pp. 378-380; ed. 2, 1935, pp. 440-443.

The specimens on which this report is founded are in my collection at the University of Washington and have been collected mostly since 1932. To Dr. Harriet Exline I am especially indebted for numerous vials of specimens from different localities. Prof. Trevor Kincaid, Mrs. Agnes D. Horn, Dr. Dora P. Henry, and Mr. William Rueter have likewise been of considerable assistance, and Mr. Ervin F. Dailey, Mr. Robert Flock, Miss Gertrude Hoppe, Miss Rita McGrath, and Mr. Raymond Nichols have contributed specimens.

Ligidium gracile Dana

(*tenue* Budde-Lund)

Central California (Santa Clara) to southeastern Alaska (Sitka) west of the Cascade Mountains. In Washington this species is not in any sense littoral as claimed by Van Name (loc. cit., p. 34), but is confined to very moist situations in dense woods from sea level to 4500 feet.

WASHINGTON: Lewis and Clark State Park, Mt. Rainier (Narada Falls), Mount Vernon, Olympia, Olympic Hot Springs, San Juan Islands (Doubleneck), Seattle, Snoqualmie Falls.

Oniscus asellus L.

WASHINGTON: Seattle on the University Campus.

Porcellio scaber Latr.

This is the dominant sow bug of the Pacific Northwest. Arcangeli (Boll. Lab Zool. Gen. e Agraria, Portici **26**, 1932, pp. 127-129) believes the species to be endemic in this area, naming them var. *americanus*, and he may be correct. My own impression, however, is that the species is rather strictly confined to the vicinity of human habitations or places of human activity like bridges and picnic grounds, which would seem to show that it is an introduced species in this region. It is certainly very far from ubiquitous in the middle west.

The two color varieties, ab. *marmoratus* Brandt and Ratzeburg with more or less extensive pale spots, and ab. *marginata* Brandt and Ratzeburg with pale margins, are apparently likely to occur anywhere along with the typical form in varying degrees of development.

BRITISH COLUMBIA: Gold Stream (Vancouver Island).—IDAHO: Waha Lake.—MICHIGAN: Calumet—OREGON: Burns, Condon, Cornelius, Corvallis, Glendale, Pen-

dleton, Portland, Port Orford, Tillamook.—WASHINGTON: Asotin, Bay Center, Chatteroy, Chenook, Cle Elum, Coulee City, Granite Falls, Kahlotus, Lewis and Clark State Park, Mora, Mount Vernon, North Bend, Olympia, Oysterville, San Juan Islands (Blakeley Is., Brown Is., Doubleneck, Flattop Is., Friday Harbor, Mt. Constitution, Skipjack Is.), Seattle, Snoqualmie Falls, Tenino, Warm Beach, Whidby Is. (Sunnyside).

Porcellio littorina Miller

Described by Miller (loc. cit., **41**, 1936, p. 168, figs. 14-15) from Bay Farm Island, Alameda, California, under rocks above the high tide line. This is probably an American species and may be definitely associated with the sea shore. It is distinguished by the penultimate segment of the antenna being only one-third the length of the ultimate segment. The specimens of the type series appear to be more prominently spotted with brown than the single Washington specimen which, in alcohol, is nearly white.

WASHINGTON: Bay Center, a single specimen collected by Trevor Kincaid just above the high tide line.

Porcellio laevis Latr.

ARIZONA: Tuscon.—MONTANA: Pipestone Hot Springs.

Porcellio spinicornis Say

MICHIGAN: Eagle Harbor in the rocks along the Lake Superior shore.

Porcellionides pruinosus Brandt
(*Metoponorthus pruinosus* Brandt)

MICHIGAN: Detroit.—TENNESSEE: Chattanooga.

Cylisticus convexus DeG.

Van Name (loc. cit., p. 261) suggests that this species may be indigenous in eastern North America, since it occurs in "places more or less remote from human habitations, as well as about the latter," but my records do not tend to confirm this.

The series of 18 specimens from Ruby Falls Cave on Look-Out Mt. near Chattanooga, Tennessee, were taken in a cave that was said to have no natural entrance. The color of these specimens as contrasted with those taken in normal situations is decidedly pale, varying from almost pure white to only a shade or two lighter than normal. The eyes are pigmented as is normal and otherwise they do not appear to differ from normal specimens.

MICHIGAN: Ann Arbor, Calumet, Detroit, Eagle Harbor.—ONTARIO: Bois Blanc Is. (Essex Co.).—TENNESSEE: Chattanooga, Ruby Falls Cave on Look-Out Mt. near Chattanooga.—WYOMING: Mammoth Hot Springs (Y.N.P.).

*Trachelipus** *rathkei* Brandt
(*Tracheoniscus rathkei* Brandt)

COLORADO: Canyon City.—IDAHO: Twin Falls.—INDIANA: Winona Lake.—MICHIGAN: Ann Arbor, Burt Lake (Cheboygan Co.), Rochester, Royal Oak, Sylvan Lake (Oakland Co.), Utica.—ONTARIO: Bois Blanc Is. (Essex Co.).—OREGON: Robinette.—WASHINGTON: Dry Falls (Grand Coulee), Coulee City.

Armadillidium vulgare Latr.

MICHIGAN: Ann Arbor, Detroit.—TENNESSEE: Chattanooga.—WASHINGTON: Seattle.

Notes on Two Species of Gastrotricha from Washington

MELVILLE H. HATCH

Chaetonotus chuni Voigt, known previously from Germany and Czechoslovakia, occurs in cultures prepared from material collected in a pond on the campus of the University of Washington campus in Seattle. The cultures in which it occurred were

* I am unable to follow Van Name (loc. cit., p. 262) in rejecting *Trachelipus* Budde-Lund 1908 because it was proposed without diagnosis. Previous to 1931 a diagnosis was not required to establish a generic or sub-generic name.

obtained by placing small pieces of pond weed in dishes containing sufficient water to prevent the formation of a bacterial scum. They were accompanied by Amoeba, Arcella, Centropyxis, and Vorticella, and were present in the sixth week of the culture. *Chaetonotus chuni* Voigt (Voigt, Zool. Anz. **25**, 1901, p. 37.—Collin, Süsswasserfauna Deutschlands **14**, 1912, pp. 247, 249, fig. 282.—Grunspan, Ann. Biol. Lacustre **4**, 1909-1910, pp. 260, 295, fig. 37) runs to *C. similis* Zelinka in Ward's key (Ward in Ward and Whipple, Fresh-water Biology 1918, p. 626) and differs from it by its stouter form, the absence of a "neck," and the fact that the accessory barbs on the dorsal spines are distant from the apex of the spine.

I find in the same cultures *Lepidoderma squamatum* Dujardin (Grunspan, loc. cit., p. 248, fig. 10; Ward, loc. cit., p. 625, fig. 967), previously known from Germany, France, England (?), Austria, Rumania, and New Jersey.

UNIVERSITY OF WASHINGTON,
SEATTLE, WASHINGTON.

Bibliofilm Service in Geological Survey

To give research workers throughout the country access to further materials for their work, a Bibliofilm Service has been opened in the Library of the Geological Survey, United States Department of the Interior, Washington, D. C. Through the courtesy of Guy E. Mitchell, Librarian, it is now possible for a scholar anywhere to order copied any properly copyable extracts from the quarter million books, journals and rare materials in this leading scientific library, as well as many of its fifty thousand maps.

Bibliofilm Service is operated on a non-profit basis by the American Documentation Institute under a cooperative agreement with the Library of the U. S. Department of Agriculture, and also maintains copying installations in that Library and the Army Medical Library. It acts as a national clearing house for copying orders for research materials, filling them through its own and other services, for materials located in substantially all Washington and Baltimore libraries, bureaus and institutions and in other cities here and abroad.

Copying is done in either of two forms; microfilm (a series of still images on 35 mm. standard safety photographic film comfortably usable in reading machines now widely available) at 1 cent per page, plus fixed service charge of 20 cents; or in the form of photoprints (6 x 8 in. legible without optical aid) at 10 cents per page, plus service charge of 20 cents.

Inquiry should be made in the form of a definite order for the copying of specific materials; if available and properly copyable the order will be filled. Order blanks making a letter unnecessary are available free on request. Remittance must accompany order, or an amount of $5 or more may be sent to open the usual deposit account which saves the bother of remitting small sums. Information on reading machines may be obtained from Science Service, Washington, D. C., who also supply a hand viewer invented by Dr. Atherton Seidell, suitable for reading short extracts, at $1.50.

The additional resources now opened to research workers everywhere, through Bibliofilm Service in the Geological Survey Library, comprise everything properly copyable among over 250,000 volumes including geology, mining, paleontology, mineralogy, chemistry, 50,000 geologic and other maps, United States and foreign; some 1200 foreign and domestic periodicals and serials including reports of State Surveys, and Mining Bureaus, all governmental publications on the above subjects, and the geological publications obtained by exchange from every foreign government.

There are many surprising finds; items not duplicated in any other American library; some exceedingly rare and useful aggregations.

Remittance for copying material in the Geological Library, or material in other fields located in other libraries, should be made payable to American Documentation Institute and all orders for copying should be mailed therewith to Bibliofilm Service, care U. S. Department of Agriculture Library, Washington, D. C.

Book Reviews

GRAPTOLITHINA von O. M. Bulman. Handbuch der Paläozoologie. Band 2D, Lieferung 2, 1938, 92 pp., 42 groups of figures. Gebr. Borntträger in Berlin, price 15 RM. In English.

By RUDOLF RUEDEMANN

Dr. Bulman, one of the leading authorities on graptolites who since 1927 is publishing an excellent monograph of the Dendroidea (Paleontological Society, London) has undertaken to write a comprehensive survey of the graptolites, an extinct class of invertebrates that is of equal interest to the paleontologist and the stratigrapher.

The work is particularly valuable to the paleontologist through the numerous structure-diagrams, especially of Dendroidea made from serial sections by Wiman. While the author has clearly perused the entire literature, he has remained strictly conservative in the presentation of the many problems still under discussion.

The classis Graptolithina is defined as consisting of extinct, colonial, marine organisms, possessing a chitinoid exoskeleton in the form of a series of cups (or thecae), variously arranged along one or more branches (or stipes), the colony (or rhabdosome) originating in a conical sicula. It is divided into the generally accepted orders: Dendroidea Nicholson and Graptoloidea Lapworth emend. auctt.

Order Dendroidea. The Dendroidea are mostly sessile, erect forms with dendroid rhabdosomes and three types of individuals. The first chapter on *morphology* is the most interesting and important one on account of the numerous diagrams showing the relations of the different elements of the rhabdosome, the hydrothecae, the bithecae and the budding individuals; further the thecal grouping and the mode of branching.

The *budding-individuals* are tubular cavities within the stipe, each of which gives rise to a hydrotheca, a bitheca and a budding individual of the next generation. The budding-individual itself never opens to the exterior except presumably at the growing end of the stipe. Functionally, the budding individuals must have been solely concerned with the propagation of the stipe. Bulman states that if they had a separate entity as Wiman maintains, the mode of propagation recalls that of the hydrotuba stage of the Scyphozoan Stephanoscyphus; if not, the continuous chain of budding individuals suggest something functionally comparable with the coenosarc of the Hydrozoa.

The *bithecae* are smaller and less conspicuous than the hydrothecae and open on alternate sides of the hydrothecae. They are not always easily detected from the exterior. They have been considered as nematophores and as gonangia and Bulman would also place the hemispherical appendages of Marsipograptus considered as Polyzoan ooecia by Ulrich and Ruedemann with the bithecae. The non-committal term "bitheca" finally adopted by Holm is held to be best expressing our present knowledge.

The relation of the bithecae to the hydrothecae is quite variable as they bend over before or behind the hydrothecae in various genera and original diagrams are given to illustrate this complex relationship.

The *hydrothecae* of the Dendroidea are described as relatively constant in form as compared with the thecal elaboration of the Graptoloidea. Variations are produced by isolation of the hydrothecae, apertural denticulation and spines. The hydrothecae are considered as almost certainly corresponding to the thecae of the Graptoloidea and are presumably representing the nourishing individuals of the colony.

A separate chapter describes the *thecal grouping.* This is simple in the Dendrograptidae where the hydrothecae and bithecae form a visible unit on the exterior. It becomes much more complex in those genera (Acanthograptidae) in which the thecae open as groups or "twigs" from the main stipe and which form is associated with the development of elongate tubular thecae. The different forms of grouping, often probably quite irregular, have not yet been studied. In some forms anastomosis of branches seems to be accompanied by an exchange of individuals as in Koremagraptus Bulman.

The *shape of the rhabdosome* and the *mode of branching* is discussed in a further chapter. Also here a wide variation of irregularly branched or dendroid forms, typified by Dendrograptus, to a regular cyathiform or conical type, as seen in the rhabdosome of Dictyonema, is recognizable. Branching may be either dichotomous or, less commonly, lateral in type. The actual mechanism of branching has been so far studied only in a few species and is not well known. There seems to be wide variation in the hydrothecae of the older generation taken over into the new branch. Two diagrams of the mode of branching in two forms of Dictyonema are given.

A brief chapter is given to the *mode of attachment*. The sicula is originally provided with a more or less long nema, which may end in a disc of attachment. Later various root-like appendages are formed which usually envelop the sicula and which served to attach the rhabdosome to the sea bottom or shells. Some were probably pendent and lived attached to floating sea-weed in the manner of the true graptolites.

The *ontogeny*, or rather *astogeny*, is studied most reliably by serial sections. Only two species *Dictyonema cavernosum* and *D. flabelliforme* have been studied by this method. Wiman found in the former species above the attachment disc a theca and a budding individual. He inclines to the view that an older, non-chitinized and free-swimming individual had produced both the theca and hydrotheca. Bulman compares the first theca with the sicula of the Graptoloidea and that of *D. flabelliforme*.

In the interesting chapter on *ecology* it is shown, that while the great majority of Dendroidea undoubtedly were attached to the bottom, some as *Dictyonema flabelliforme*, which is probably ancestral to the Graptoloidea, may have had a pseudoplanktonic or epiplanktonic mode of existence, having been attached to seaweeds by the nema and attachment disc or the various forms of roots described of that species. The ecological interpretation of these features is an almost untouched field.

Geographical and geological distributions. In contrast to the Graptoloidea the dendroid graptolites are of sporadic distribution and little zonal value, the latter mostly on account of their comparative rarity. *Dictyonema flabelliforme* recorded from a well-defined horizon of northwest Europe and from both Pacific and Atlantic coasts of North and South America is a shining exception.

The time range of many of the Dendroid genera is extraordinarily long, in marked contrast to the majority of the graptoloid genera.

The *phylogeny* of the Dendroidea is still unknown. The stratigraphical distribution is of little assistance for most of the important genera have approximately co-equal ranges in time and the interrelations of the genera are still very uncertain. *Dictyonema flabelliforme* was long considered as an ancestral form, but the discovery of a large Upper Cambrian fauna in North America, mostly composed of Dendrograptus, places the relatively simple Dendrograptus in line as an ancestral type.

In the chapter on *Systematics* are distinguished the following families:

Dendrograptidae Roemer with the genera *Dictyonema* Hall, *Reticulograptus* Wiman, *Ptiograptus* Ruedemann, *Callograptus* Hall, *Dendrograptus* Hall, *Desmograptus* Hopkinson, *Marsipograptus* Ruedemann, *Aspidograptus* Bulman, ? *Syrrhipograptus* Poulsen.

Acanthograptidae nov. with the genera *Acanthograptus* Spencer, *Thallograptus* Ruedemann, *Koremagraptus* Bulman, *Palaeodictyota* Whitfield, ? *Inocaulis* Hall.

Ptilograptidae Hopkinson. *Ptilograptus* Hall.

Cyclograptus nov. *Cyclograptus* Spencer, *Galcograptus* Wiman, *Discograptus* Wiman, ? *Calyptograptus* Spencer, ? *Rhodonograptus* Počta.

As Dendroidea of uncertain systematic relations are considered:

Mastigograptus Ruedemann, *Chaunograptus* Hall, *Ascograptus* Ruedemann, *Haplograptus* Ruedemann.

As genera of uncertain relations that have been referred to the Dendroidea are considered:

Buthograptus Hall, *Cactograptus* Ruedemann, *Ceramograptus* Hudson, *Diplospiro-*

graptus Ruedemann, *Medusaegraptus* Ruedemann, *Thamnograptus* Hall, *Protovirgularia* McCoy.

Order Graptoloidea. The Graptoloidea are mostly planktonic or pseudoplanktonic with pendent rhabdosomes of few stipes and generally composed of hydrothecae only. The relation of the direction of growth of the branches (from pendent through horizontal to scandent) affords an important basis of subdivision. Likewise the number of stipes, there being a general tendency towards reduction of the stipes. Frech's division into two orders Axonolipa and Axonophora based essentially on the presence or absence of an "axis", that really reflects the degree of scandency attained by the rhabdosome, is not accepted.

The *sicula* is described from the observations of Wiman and Kraft as composed of two portions, an apical and apertural one, termed prosicula and metasicula by Kraft, and the formation of the virgella and apertural spines noted. It is suggested that judging from the difference in size and shape of the sicula from the hydrothecae it contained an individual somewhat differing in character from the hydrothecal individuals.

The *hydrothecae*, more or less overlapping tubes, are fully described in their morphologic elaboration which has proven of great importance, especially to the British authors, for family and generic distinction. This elaboration begins with a slight sigmoidal curvature of the ventral wall and leads to forms with strongly curved or angulated tubes, introverted and introtorted apertures and isolation of the apertural region of the tubes. The curvature and isolation is carried to extreme length in the Monograptidae. An excellent series of diagrams illustrates the various thecal forms.

The *common canal.* The problem of the presence or absence of a common canal in regard to which different views are held, is discussed and the evidence favoring the existence of a coenosarc structure presented. It is concluded that the typical dendroid thecal structure persisting in some Graptoloidea (Clonograptus and Bryograptus), leaving little doubt that the Graptoloidea are descended from the Dendroidea, lets one expect that a coenosarcal structure also persisted in the soft parts of the Graptoloidea. Minor problems as the relations of the virgula to interhecal septa in biserial graptolites and the growth-lines of the periderm are concisely presented.

Under the heading of the *nema* or *virgula* the development of the nema into the virgula or central tube in biserial forms is described and the relation of the virgula to the medium septum set forth, especially also in regard to the different arrangement of the Retioloidea. Here also the occurrence of a terminal *float* at the distal extremity of the virgula in some forms is noted and the occurrence of *synrhabdosomes* or stellate groups of rhabdosomes as well as the occurrence of a central float, described by some authors, briefly discussed.

The next chapter takes up the important features of the *branching* of the rhabdosome and states that while lateral branching occurs dichotomous branching is more common and the marked tendency to reduction in the number of branches and its possible causes (better food supply to the hydrothecal individuals or symmetry to better balance the suspended rhabdosome) discussed.

In the chapter on *special features of the rhabdosome* the lateral and dorsal spines, the localized thickening of the periderm, floats, vesicles etc. are described in regard to their origin, distribution and function.

The *muscle-scars* observed by Ulrich, Ruedemann and Haberfelner are briefly mentioned and next the *structure and composition of the periderm* taken up. Sollas' view that the periderm consisted of three layers is provisionally accepted and chitin considered as the substance of the periderm according to the chemical tests of Kraft.

The *development* is both so intricate and important a subject that it is elaborately dealt with and four types, viz. Dichograptid, Leptograptid, Diplograptid and Monograptid are fully described and excellently illustrated by diagrams.

Under *physiology* the grapto-gonophores and reproduction sacs of earlier authors and the "verticels of oval capsules" of Ruedemann are described and partly figured and the problem of their function left open.

The *significance of the sicula in the life-cycle of the Graptoloidea* is the heading of

another interesting chapter. It is considered still very uncertain whether there was an alternation of generations and the probability is mentioned that the reproduction which resulted in the embryo was asexual, despite the distinctive appearance of the sicula and it is tentatively suggested that this propagation of new colonies was perhaps accomplished by the sicular individual, and that herein may lie an explanation of the morphological difference between the metasicula and the hydrotheca.

We should like to enter deeper into the fascinating chapter of *ecology* but space forbids. It may suffice to say that Bulman holds with more recent authors that the Graptoloidea in distinction to the Dendroidea led for he most part a pseudoplanktonic life and that some of the later species had acquired the structures necessary for a truly planktonic mode of existence.

The black shale, which is characteristic as the graptolite facies, is considered as indicating quiet but not necessarily deep water, as the lack of bottom circulation necessary to preserve the purely planktonic or pseudoplanktonic fauna found in the pure graptolite shales may also occur in shallow lagoons and embayments. The reviewer's recent announcement of the occurrence of deep sea radiolarians in graptolite-bearing cherts would seem to indicate the formation of graptolite shale in both litoral and abyssal depths.

Under the *geographical and geological distribution*, the subject of the next chapter, it is set forth that the graptolites on account of their planktonic or pseudoplanktonic life have a world-wide distribution and that they permit more widespread correlation than any other organisms, at least of Lower Paleozoic age. However, the zonal successions are not indicated over very wide areas, and may even occasionally show local peculiarities which suggest that sometimes the graptolites underwent local evolution of comparatively short duration in more or less enclosed seas or embayments. The reviewer has gathered evidence of wider differences in the faunas of the Atlantic and Pacific basins.

The Graptoloidea appear in late Upper Cambrian time and die out, with rare exceptions in late Silurian time.

The number of graptolite zones has risen in Great Britain from Lapworth's 20 zones to 36 in the Monograph of British Graptolites (19 zones are so far distinguished in the Ordovician of North America) and is still constantly rising in Europe, America, Asia and Australia. Using the investigations of radioactivity Bulman finds 40-50 million years as the period of deposition of the 20 Silurian graptolite zones, so that the average length of a short-ranged graptolite species would be rather more than two million years.

The various trends in graptolite evolution as reduction in number of stipes, change in direction of growth of stipes, and particularly also the various types of thecal elaboration make the graptolites exhibit "programme evolution" perhaps better than any other group of organisms.

Phylogeny. We cannot begin to discuss here the elaborate chapter on phylogeny as there is no space to enter into necessary details, but wish to emphasize the splendid illustration of the chapter by large series of original diagrams which will prove fundamental in later studies.

In the chapter entitled *Stratigraphical Conclusions* four successive graptolite faunas are distinguished, viz. 1) Dichograptid fauna (Tremadocian and Lower Ordovician) 2) Leptograptid fauna (Glenkiln shales, Normanskill, Lower Dicellograptus, 3) Diplograptid fauna (Hartfell shales, Canajoharie and Utica, Middle and Upper Dicellograptus shales, etc.) 4) Monograptid fauna (Silurian).

The last chapter of the general introduction to the Graptoloidea is the important one on *The Affinities of the Graptolites*. Here the author first surveys the various hypotheses advanced since Linnaeus' time, then sets forth the salient features in the structure and development of the graptolites and arrives finally at the view that detailed comparison of the graptolites with any living class has not proved fruitful of results, but if they are to be placed in some existing phylum (which seems a reasonable sup-

position) it is perhaps as a separate class of the Coelenterata that their assemblage of characters can most readily be accommodated.

In a postscript the author sets forth Professor R. Kozlowski's conclusion, recently announced in a preliminary paper, viz. that the existence of fully-chitinized stolons inside the stolothecae which give rise to the triad of buds, and the structure of the periderm, exclude the graptolites from either the Coelenterata or the Polyzoa and place them principally on the histology of the periderm and method of budding with the Pterobranchia, an isolated small group of animals of unknown relationship, formerly placed with the bryozoans, but now preferably appended to the Enteropneusta. A. Schepotieff had already in 1905 indicated the possible relationship of the graptolites with Rhabdopleura, one of the few Pterobranchiate genera. It may be mentioned here that E. Stechow in 1920 has suggested a striking resemblance between the last graptolites, notably Rastrites with Dinotheca, another aberrant and isolated genus which is placed with the hydrozoans.

The last thirty pages describe the *Systematics* of the Graptoloidea with brief diagnoses of all and diagrams of most genera.

The Graptoloidea are divided into families, Frech's suborders Axonolipa and Axonophora not being accepted. The first very large family *Dichograptidae* Lapworth is subdivided into groups of I) Multiramous and II) Pauciramous forms: the former again into sections of genera with a) dichotomous branching *Temnograptus* Nicholson, *Anomalograptus* Clark, *Calamograptus* Clark, *Hermannograptus* Monsen, *Anthograptus* Törnquist, *Loganograptus* Hall, *Dichograptus* Salter, *Staurograptus* Emmons, *Anisograptus* Ruedemann, b) dichotomous and lateral branching: *Holograptus* Holm, *Schizograptus* Nicholson, *Trochograptus* Holm, *Goniograptus* McCoy, *Brachiograptus* Harris and Keble, c) branching mainly lateral: *Bryograptus* Lapworth, *Trichograptus* Nicholson, *Pterograptus* Holm, *Sigmagraptus* Ruedemann.

Group II. Pauciramous forms, contains *Tetragraptus* Salter, *Phyllograptus* Hall, *Triograptus* Monsen, *Didymograptus* McCoy, *Atopograptus* Harris, *Isograptus* Moberg, *Macandrograptus* Moberg, *Oncograptus* T. S. Hall, *Cardiograptus* Harris & Keble, *Azygograptus* Hopkinson and Lapworth.

The second family *Corynograptidae* Nicholson & Lapworth, of doubtful affinities, is monogeneric.

The family *Leptograptidae* Lapworth comprises the genera *Leptograptus* Lapworth, *Nemagraptus* Emmons, *Amphigraptus* Lapworth, *Pleurograptus* Nicholson, *Syndyograptus* Ruedemann.

The family *Dicranograptidae* Lapworth contains *Dicellograptus* Hopkinson and *Dicranograptus* Hall.

To the family *Diplograptidae* Lapworth belong *Climacograptus* Hall, *Diplograptus* s. str. McCoy (*Mesograptus* Elles & Wood) *Amplexograptus* Elles & Wood, *Orthograptus* Lapworth, *Glyptograptus* Lapworth, *Petalograptus* Suess, *Cephalograptus* Hopkinson, *Akidograptus* Davies, *Cryptograptus* Lapworth, ? *Trigonograptus* Nicholson, ? *Skiagraptus* Harris.

The family *Glossograptidae* Lapworth embraces *Glossograptus* Emmons, *Retiograptus* Hall, *Lasiograptus* Lapworth (including Thysanograptus Elles & Wood), *Hallograptus* Lapworth, *Nymphograptus* Elles & Wood, *Neurograptus* Lapworth.

To the family *Retiolitidae* belong *Retiolites* Barrande, *Stomatograptus* Tullberg, *Gothograptus* Frech, *Phlegmatograptus* Elles & Wood and *Archiretiolites* Eisenack.

The family *Dimorphograptidae* Elles and Wood contains *Dimorphograptus* Lapworth and *Raphidograptus* Bulman.

The family *Monograptidae* Lapworth contains *Monograptus* Geinitz (with numerous synonyms), *Cyrtograptus* Carruthers, *Diversograptus* Manck, *Abiesgraptus* Hundt, *Linograptus* Frech.

As Graptoloid genera *incertae sedis* are listed: *Protistograptus* McLearn, *Protograptus* Matthew, *Strophograptus* Ruedemann and *Triaenograptus* T. S. Hall.

A selected bibliography concludes the hand-book.

Dr. Bulman is to be congratulated on and thanked for furnishing all graptolite-students with this hand-book. It affords in concise form such a comprehensive survey of all that is known on graptolites that it will prove a great boon and a necessary tool to every one who wishes to work with this fascinating and important class of fossils. It is an especially welcome guide-book to the reviewer for the monograph of the graptolites of North America on which he has been engaged for a decade.

N. Y. State Museum,
Albany, N. Y.

The Bird Life of Louisiana. By Harry C. Oberholser. Bulletin No. 28, State of Louisiana, Department of Conservation, New Orleans, June, 1938. xii+834 pp., illustrated.

This octavo volume gives a complete account of practically all 430 species and subspecies of birds known to occur in Louisiana and of 22 additional birds possibly found in the state thus exceeding by 77 forms the previously recorded avifauna. The book is attractively printed and illustrated by 45 excellent halftone plates, most of them showing photographs taken by Alfred M. Bailey. Eight plates are in colors, from paintings by various well known bird artists, the colored frontispiece illustrating that well-nigh extinct species, the Ivory-Billed Woodpecker.

The opening pages are devoted to a description of Louisiana as a habitat for birds, followed by a brief chapter on migration of birds, one on a calendar of bird migration in the state and a few pages on the protection of birds. The breeding habits, dates of migration, rarity or abundance, songs and notes are given for each species. Unfortunately the book is lacking in technical descriptions as well as text figures making for ready identification.

A notable feature is the separation of the vultures, hawks, etc. from the owls by nearly 200 pages, a treatment to be expected from so well known a systematic ornithologist as the author. The appearance of several changes in nomenclature, all of which are undoubtedly justified, is of questionable taste in a work lacking any synonymy for the various species.

Appended are a complete bibliography, arranged chronologically rather than according to authorship, as well as complete indices of species and authors. The volume should prove of interest and value to all Louisiana ornithologists and those of other states.—Marcus Ward Lyon, Jr.

Comparative Studies on Trematodes (Gyrodactyloidea) from the Gills of North American Fresh-water Fishes. By John Dary Mizelle. Univ. Ill. Bull. 36 (8):1-69, 5 pls. [Illinois Biological Monographs, 17(1)] 1938.

Despite the fact that a number of papers on the monogenetic trematodes of North American hosts have appeared during the past few years, only a few are monographic in scope; the present paper by Mizelle is one of these. While dealing largely with descriptions of 21 species of Tetraonchinae from fresh-water fishes of Illinois, the paper contains an adequate discussion of the morphology of the trematodes of this subfamily as well as a summation of the characters of the superfamily Gyrodactyloidea. Useful keys to the genera of Tetraonchinae and higher groups are included. One of the most useful features of the paper is a digest of the greater part of the literature dealing with the economic importance of the ectoparasitic flukes and of the measures recommended for their control. Five plates are appended giving adequate drawings of the species described and of the parts most used in making identifications. The author promises for the future a paper dealing with a revision of the North American fresh-water genera of Tetraonchinae. It is regrettable that the present paper was not expanded to include such a revision.—E. W. Price.

PROBLEMS OF ANIMAL ECOLOGY. By F. S. Bodenheimer. Oxford University Press, London, Humphrey Milford. 1938. vii + 183 pp., 28 figs. $4.00.

Animal ecology is still a relatively young science and is far from having outgrown its descriptive stage, although many attempts at causal interpretation have been made. Many problems are stagnant and await a new attack. The author has selected a number of these which are urgently in need of reconsideration and which represent the often neglected fields bordering physiology and genetics. One chapter is devoted to each of the following sets of problems: physiological and ecological life-tables and connected problems; the life-history and its ecological interpretation today; what really occurs in the *Drosophila* bottle? a further approach to a complete population analysis; biological equilibrium in nature and biological control; is the animal community a dynamic or a statistical conception? the interaction of environment and heredity within the organism.

The author pleads strongly for the relinquishing of the frequently existing "orthodox attitude of a large majority of present-day biologists" in the approach to these problems, especially as regards the interaction of heredity and environment. Although the available literature is carefully considered, much original material is presented, thus lifting the book definitely above the level of a review. Most of the illustrations were "prepared especially for this book with a view to filling blanks in the ecological literature." Despite its small size, the book offers very stimulating, though by no means easy, reading, "but easy reading should be avoided in the present stage of mind of animal ecology, where the formation of theories is so easy and the basis of facts yet so narrow." The reader may not always share the opinions of the author, but he will readily concede that the book will serve to stimulate the advance of our knowledge of animal ecology.—TH. JUST.

GRUNDRISS DER INSEKTENKUNDE. Von Hermann Weber. Gustav Fischer, Jena. 1938. xii + 258 pp., 154 figs. Bound RM 13,50.

In recent years several excellent texts covering the whole field of entomology, or certain phases of it, have made their appearance. They are, however, somewhat too extensive to present a suitable introduction. This "Grundriss" was prepared, therefore, to meet this need. An effort was made to review with equal care all fields of entomology without giving space to the discussion of zoological principles of a general character. The illustrations are in the characteristic style of the author, or carefully selected from other sources.

A short introduction shows the relationship of the insects to other groups and gives their phyletic background. The first part of the book is concerned with the embryology, structure and function of the insect body, the second is devoted to the principal groups, whereas the third part comprises an exposition of the ecology of insects in its broadest sense. A concluding chapter deals with the relations of insects and man. A concise bibliography suggests additional sources of information.

The book represents undoubtedly the best available brief treatment of entomology. —TH. JUST.

ALGAE, THE GRASS OF MANY WATERS. By Lewis Hanford Tiffany. Charles C Thomas, Springfield, Illinois. 1938. xiii + 171 pp., 41 pls. (2 colored), 12 figs., 4 tables. $3.50 postpaid.

Whereas fungi are frequently treated in books intelligible to many non-botanists, algae apparently do not enjoy similar popularity. Consequently, the author prepared an essentially non-technical book attempting to make the subject as palatable as possible, even introducing figures from the comic strips. Yet the information brought together

by careful selection and drawn from long personal acquaintance with these organisms is very valuable and certainly offers interesting reading. The plates and illustrations are taken from various acknowledged sources (except Plate 4) or were prepared especially by the author and Celeste Taft. It is unfortunate that Plate 2 was not subjected to the same careful treatment afforded to other composite illustrations. The book can conveniently be characterized as a good exposition of the intricate physiology and ecology of the algae, though structural features and their relationships are not overlooked. Instructions for the collection and study of algae aim to arouse active interest in these plants.—TH. JUST.

THE STRUCTURE OF ECONOMIC PLANTS. By Herman E. Hayward. Macmillan, New York. 1938. x + 674 pp., frontispiece, 340 figs. $4.90.

In comparison to available works on plant anatomy, the present volume contains a relatively short treatment of General Anatomy (Part one, pp. 1-109) whereas the bulk of the book (Part two) and a promised second volume are devoted to detailed accounts of selected economic plants. The selection of the species and the space afforded them are based on their economic importance, their fitness as types of the particular families represented by them, and their morphological complexity. The numerous excellent illustrations were obtained from published sources or prepared by the author and associates; a rather large number of these are diagrams of the root-stem transition zones. Free use was also made of the literature, though much important material, especially that relating to general anatomy, was apparently overlooked. Thus these chapters do not seem to equal those of Part two in presenting an adequate picture of our present knowledge. Throughout the work emphasis is placed on developmental anatomy, and general morphology receives, in some instances, comparatively scant attention. Approximately 30 pages are devoted to each species and the treatment adopted is fairly uniform. Though only the most important economic plants are included, the book is likely to be consulted frequently as a reference work apart from its possibilities as a text. The bookmanship is excellent and highly praiseworthy.

—TH. JUST.

FEATHERS AND FUR ON THE TURNPIKE. By James R. Simons. The Christopher Publishing House, Boston. 1938. 148 pp., 10 pls. Cloth $1.75.

Over a period of ten years, records of casualties of birds and mammals were made by the author while driving through the northeastern states and studying specimens brought to his "studio of feathers and furs". These facts and the conclusions based upon them are contained in Part I "A Study of Wildlife Casualties on the Highway". The figures presented are indeed appalling and the cry for careful driving and conservation is readily justifiable. Miscellaneous observations on food habits etc. are included. While the title of the book expresses fittingly the contents of Part I it leaves the reader uninformed of the nature of Part II "A Study of the Present Trends in Wildlife Conservation". In the latter, the author expresses his views on conservation which deviate often from accepted practices. They are, however, worthy of consideration on the part of those actively engaged in conservation. Disturbing to the reader is the frequent use of "Vertibrate". All responsible citizens should read this little book and help to achieve the restoration, as far as possible, of our vanishing wild life.—TH. JUST.

REPRINT-SERIES

(Reprints 1, 2, 3 were issued with volume 2, reprint 4 with volume 3 and reprint 5 with volume 5).

(1) RAFINESQUE, C. S.—Neogenyton. 1825 ..... $ .25

(2) ———The Natural Family of Carexides. 1840 ..... .50

(3) ———Scadiography of 100 Genera of Ombelliferous Plants, etc. 1840 ..... 1.50

(4) ———Monographie des Coquilles Bivalves et Fluviatiles de la Rieviere Ohio. Remarques sur les Rapports Naturels des Genres Viscum, Samolus et Viburnum. A Bruxelles. 1820 ..... 1.50

(5) LECONTE, J. E.—Reprints of Monographs without plates 2.50

With 42 photographic copies of unpublished plates (7x8). ..... Prices on request

———Two extra plates reproduced from originals in New York Botanical Garden ..... Prices on request

PUBLICATIONS

BAILEY, V.—Cave Life of Kentucky. 1933 ..... $ 1.25

CONANT, R.—The Reptiles of Ohio. 1938. Cloth 2.00

GREENE, E. L.—Pittonia. A Series of Papers Relating to Botany and Botanists. 5 volumes. 1887-1905 ..... 14.00

———Manual of the Botany of the Region of San Francisco Bay. 1894. Bound cloth 2.00

Unbound 1.50

———Flora Franciscana. Part 2. 1895 ..... .75

———Plantae Bakerianae. 1-3. ..... 1.30

———Cybele Columbiana. A Series of Studies in Botany, chiefly North American. (All published). 1914 ..... .75

JUST, TH. (Editor)—Plant and Animal Communities. 1939. Cloth 2.50

KISTLER, ELLEN D.—Bibliography of the Botanical Writings of Edward Lee Greene. 1936 ..... .25

LYON, M. W. JR.—Mammals of Indiana. 1936. Cloth 3.00

UTTERBACK, W. I.—The Naiades of Missouri. 1915-1016 ..... 1.50

WEATHERWAX, J.—The Phylogeny of Zea Mays. 1935 ..... .50

The University of Notre Dame

Notre Dame, Indiana, U.S.A.

THE COLLEGE OF ARTS AND LETTERS
THE COLLEGE OF SCIENCE
THE COLLEGE OF ENGINEERING
THE COLLEGE OF COMMERCE
THE COLLEGE OF LAW THE GRADUATE SCHOOL
THE SUMMER SESSION

The University of Notre Dame, the largest boarding school in the world, is located in northern Indiana adjacent to the industrial city of South Bend and eighty-six miles east of Chicago. There are two lakes on the 1,300 acre campus surrounded by beautiful groves, making an ideal setting for the pursuits of the scientist and naturalist.

For a Bulletin or other information, address

THE REGISTRAR - - Notre Dame, Indiana

Publications in Mediaeval Studies

The University of Notre Dame

VOLUME I—The Works of Peter of Poitiers, Master in Theology and Chancellor of Paris (1193-1205). By Philip S. Moore. 1936. Pp. ix-218. A critical study of the works of "the most faithful pupil of Peter Lombard." Cloth, $2.25; Paper, $1.75.

VOLUME II—Commentarius Cantabrigiensis in epistolas Pauli e schola Petri Abaelardi: 1. In epistolam ad Romanos. By Arthur Landgraf. Critical text and notes. 1937. Cloth, $2.25; Paper, $1.75.

VOLUME III—Petri Pictaviensis allegoriae super tabernaculum Moysi. By Philip S. Moore and James A. Corbett. 1938. Pp. xxiii-214. Critical text and notes. Cloth, $2.25, Paper, $1.75.

IN PREPARATION—Commentarius Cantabrigiensis in epistolas Pauli e schola Petri Abaelardi: 2. In epistolas ad Corinthios, Galatas, et Ephesios. By Arthur Landgraf. Critical text and notes.

Petri Pictaviensis sententiarum libri quinque. By Philip S. Moore, Marthe Dulong and Joseph N. Garvin. Critical text and notes.

Prepositini cancellarii Parisiensis summa theologica. By Philip S. Moore and Marthe Dulong. Critical text and notes.

Prepositini cancellarii Parisiensis summa contra hereticos. By James A. Corbett and Joseph N. Garvin. Critical text and notes.

ADDRESS: Publications in Mediaeval Studies, The University of Notre Dame, Notre Dame, Indiana (U. S. A.).

The University Press, Notre Dame, Indiana